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FURTHER OBSERVATIONS ON THE ECOLOGY OF CENTRAL ICELAND

BY P. FALK

(*With Plates* 1 *and* 2, *three Maps and one Figure in the Text*)

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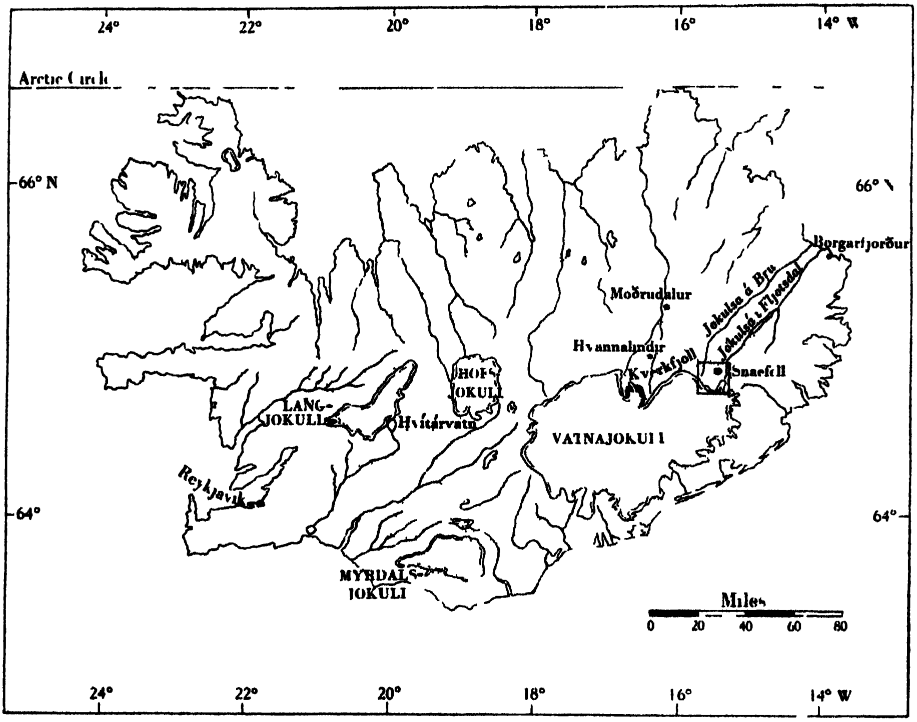
INTRODUCTION

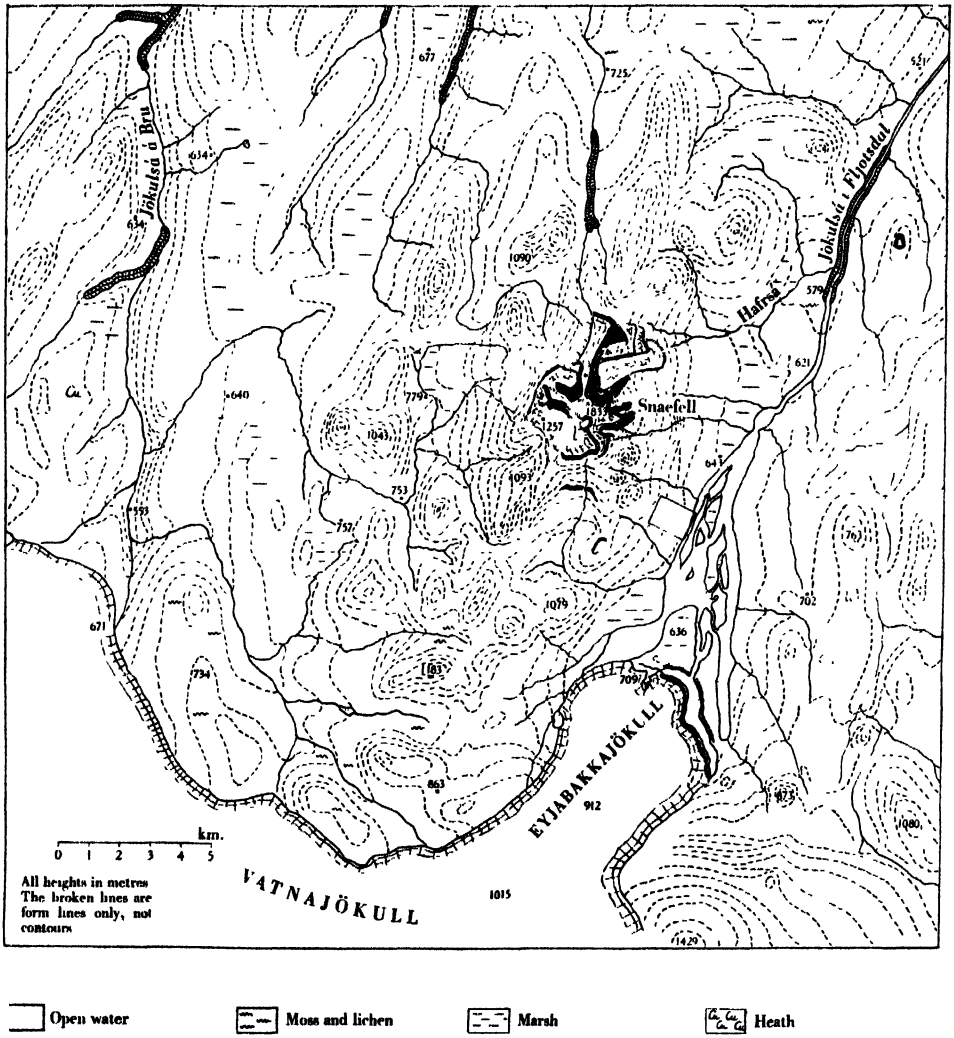
THE main interest of ecological studies in Iceland for British biologists appears to be twofold. In the first place it is of use in interpreting various problems connected with the northern element of the British fauna and flora; and in the second place it can help in giving a clearer picture of the early post-glacial conditions in Britain. These are the two aspects that have been borne in mind in the following description, rather than the comparative method which has been so ably used in the papers of Polunin (1936) and Trapnell (1933) among others.

In constructing a picture of post-glacial Britain, modern Iceland is particularly of importance, since its fauna and flora have a very close relationship with those of the British Isles and its present physical conditions (about one-tenth of its land surface being covered with ice) offer an approximate parallel to those of post-glacial Britain. In an earlier contribution to this *Journal*, an attempt was made to describe certain ecological relationships in a tract of the central highlands of Iceland on the northern edge of the largest remaining ice-cap, Vatnajökull (Anderson & Falk, 1935). This was the outcome of the Cambridge expedition of 1932 and led to further travels in the highlands in the summers of 1934, 1936 and 1937. Observations made in the western highlands around Langjokull in 1934 showed clearly that for comparison with British conditions it is essential to work in regions of pre-glacial volcanic activity rather than on the rapidly weathering post-glacial lavas which occupy much of the central highlands of Iceland. For this reason, in 1936 a preliminary expedition was made to the region of Snaefell, an extinct glacial volcano on the north-eastern edge of Vatnajökull, this area being chosen because it offered a large area of pre-glacial rock bordering directly on the largest of the ice caps and as far removed as possible from human interference. The extent and quality of the vegetation in this area so greatly exceeded what was expected from the existing descriptions that a further expedition was made to it in 1937, and the present paper is the outcome of these two expeditions.



Map 1. Iceland. The area in Map 2 is shown in a square All land 500 metres above sea-level is dotted.

The Snaefell area forms part of the central plateau of Iceland, and its outstanding topographical features can be seen from Map 2. On the south, the area under investigation was limited by the ice cap, Vatnajökull, which dominates the whole landscape and ascends from a height of 2200 ft. (670 m.) at its edge to 5100 ft. (1550 m.) 30 miles farther south. A large glacier,



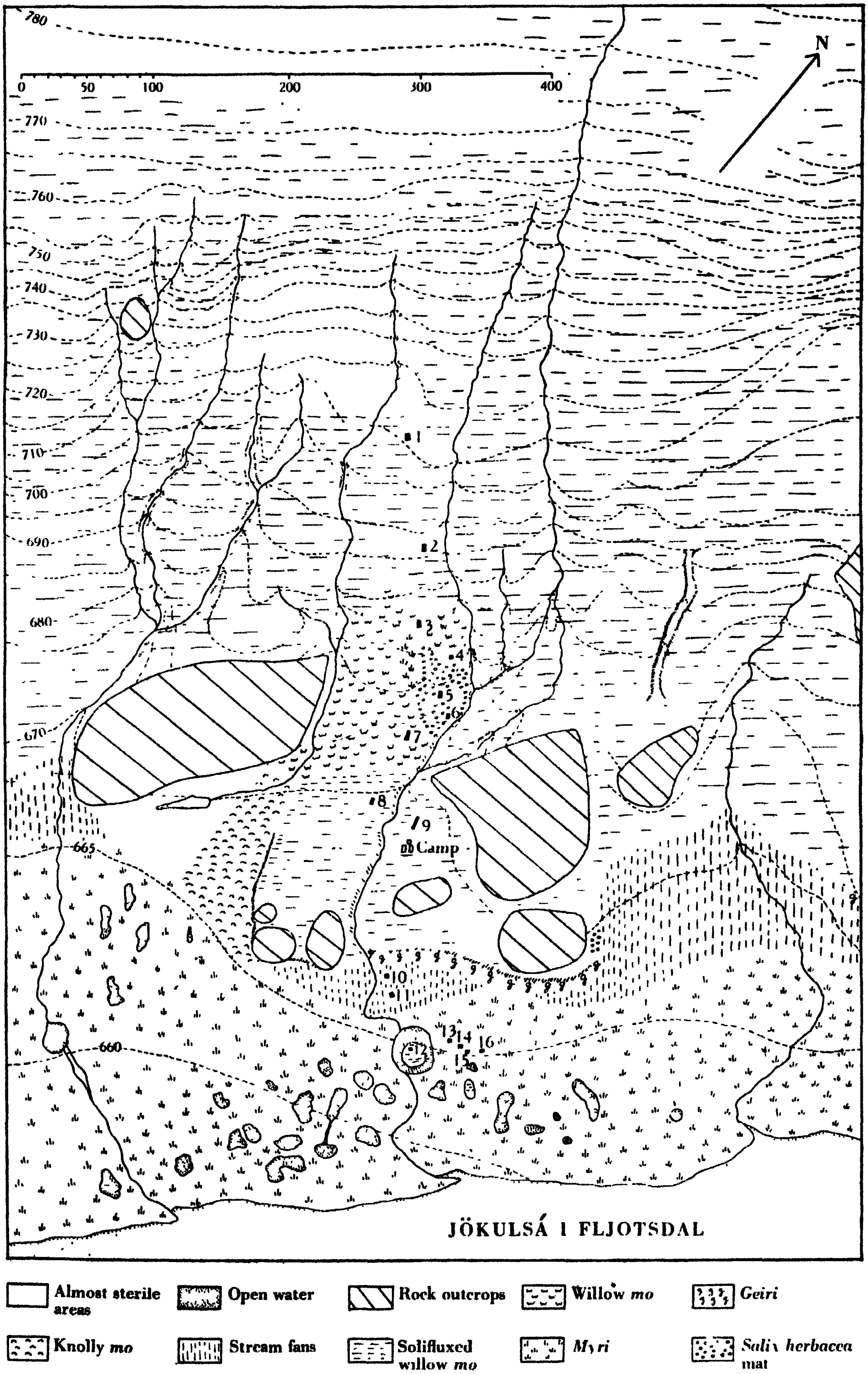
Map 2. Map of Snaefell district. (Redrawn from the Survey of the Geodetic Institute of Denmark by kind permission of the Director-General). The area in Map 3 is shown enclosed.

Eyjabakkajökull, comes down from Vatnajökull on the south-east of Snaefell, and from this glacier run the gravel-choked distribution streams of the Jökulsá i Fljotsdal, forming an eastern limit to the area. The western boundary of the area may be taken as the Jökulsá á Bru, and the northern boundary is approximately coincident with the river Hafrsá, which drains the north-eastern spurs of the Snaefell range. The whole area is a part of the highland plateau, which lies about 2000 ft. (600 m.) above sea-level. The Snaefell range stands out above the general level of the plateau, Snaefell itself attaining a height of 6050 ft. (1833 m.). The rocks are mainly basalts, breccias, tuffs and conglomerates, but there are no signs of any post-glacial volcanic activity. A close covering of vegetation persists from the valleys of the two rivers forming the boundaries of the area to within about a mile of Vatnajökull, and this vegetation is continued from the river banks over all parts of the plateau below a level of about 2400 ft. (730 m.). In the present investigations a detailed examination was made of a small representative area on the east of Snaefell (shown in Map 3), and this was supplemented by observations made throughout the larger area. The smaller area is referred to throughout as the special area.

There is no precise information available regarding the climate of the Snaefell area. The mean annual temperature of Möðrudalur, a farm 40 miles from Snaefell and at a height of 460 m. above sea-level, is −0·4° C., the mean summer temperature being 8·4° C. and the mean winter temperature −7·2° C. On account of its greater height the mean winter temperature in the Snaefell area is probably therefore not more than −1·5° C., while the mean summer temperature is probably about the same as that of Möðrudalur. During our stay of 50 days in 1937, the temperature at 10.0 a.m. varied between 6 and 18° C., while the temperature at 10 p.m. varied between 4 and 9° C. The amount of the precipitation can be deduced with even less accuracy. The nearest recording station is Borgarfjörður on the east coast, where the total annual precipitation is 46 in. (140 cm.). At Snaefell the precipitation is undoubtedly greater than this and probably exceeds 65 in. (165 cm.), since the winds are mainly northerly and easterly. More than half of this precipitation must be in the form of snow. The duration of the snow cover is known with greater accuracy from the reports of the shepherds who visit the district. The whole area appears to be covered from mid-September to mid-May, and patches of snow persist in hollows at heights of only 2200 ft. (730 m.) until the end of July.

Unlike the rest of the highlands north of Vatnajökull, the Snaefell area has been visited continuously from the times of the first settlement. It has never been permanently inhabited, though a summer dairy dating from the fourteenth century was found by Brunn high up on the mountain side. At the present time sheep are driven up to this district for summer pasture, but the great majority of these graze on the terminal moraine of Eyjabakkajökull, and the density on the hillside is far below one per acre. Apart from grazing, the area is not in any way interfered with by man, and human influence is therefore mainly of an indirect kind, such as the possible starting of erosion at sheep runs.

The only account of the district which is of importance from an ecological



Map 3. The distribution of vegetation in the special area. (Surveyed by L. H. McCabe, 1937.) Heights and distances measured in metres.

point of view is that of Thoroddsen (1895), who spent two days there in 1894. His account includes a fairly accurate description of the topography, but he underestimated the extent of the vegetation. The vegetation on the north of the mountain is described as an oasis in the central desert, whereas, in fact, it is continued directly from that of the Lagarfljot valley, and must certainly have been so in Thoroddsen's time. This oversight may be accounted for by the shortness of Thoroddsen's stay and the bad weather he experienced. Apart from this, the highlands of eastern Iceland appear to have been completely neglected by ecologists. The western highlands, however, have been excellently treated by Hansen (1930), and though he worked at a lower altitude (400 m.), his types of vegetation, which have become a standard in the recent literature of Icelandic botany, are clearly recognizable in the Snaefell area, and wherever possible have been introduced in the following account.

TYPES OF VEGETATION

Before describing the vegetation of the district, a point of some interest must be mentioned arising from the excavations which were made in order to investigate soil profiles. A series of excavations was made in the special area, and a large number of these revealed a white band about 1·5 in. (4 cm.) thick at varying depths below the surface (see Table 1). This white band resulted from a deposit of white sandy material, which has been kindly identified by Dr F. Coles Phillips of the Department of Mineralogy, Cambridge, as a non-crystalline glass and therefore a wind-borne volcanic ash. The band can be seen in Pl. 1, phots. 2, 3, in both of which it shows clearly in contrast with the dark soil above and below it. Similar deposits of ash are to be found in many places in Iceland, in some cases, e.g. Öraefajökull on the south coast, being many feet in thickness. Their investigation, however, has scarcely begun, and though it may well be possible to date some of the deposits in the future, sufficient data is not available at the present time. When these deposits of volcanic ash can be dated, much valuable information concerning such problems as the rate of soil formation will be obtained, but in the meantime they have considerable value in tracing movements of the surface layers of the soil. A comparison of the two photographs referred to above will make this clear. In the former, the ash is present as a level undisturbed layer and there has clearly been no movement of the surface soil. In the latter, however, the ash is thrown into folds, and it can easily be shown that this does not represent the original form of the soil surface, since in the first place there is no tendency for the ash to accumulate in pockets as it would if it fell on hummocky ground, and in the second place the folds occasionally are so complete that they take the form of a reversed S, a position which can only be explained by assuming that the surface has been laterally displaced.

The area chosen for detailed examination lies on the east of Snaefell and extends about 800 yards from the bank of the Jökulsá i Fljotsdal; Map 3 is

Table 1. *Data obtained from excavations*

Number of pit	Depth of water table		Depth of ash band		Depth of ice		Type of vegetation	Comments
	ft.	in.	ft.	in.	ft.	in.		
1	7	6	4	9	—		Solifluxed willow *mo*	Ash band discontinuous: poorly marked
2	3	6	1	7	—		Solifluxed willow *mo*	Ash band discontinuous: poorly marked
3	1	3	1	3	—		Willow *mo* approaching *myri*	Close vegetation without signs of solifluxion: ash band continuous, ¾ in. thick, level
4	2	6	1	1	—		Willow *mo* with slight solifluxion	Open cover. Sinuous ash band, well marked in places
5	2	10	1	1	—		*Salix herbacea* mat	No signs of solifluxion. Level, continuous ash band
6	—			8	—		*Salix herbacea* mat	No signs of solifluxion. Level, continuous ash band
7	2	0		9	—		Willow *mo* with slight solifluxion	Open cover. Ash band clearly marked; level, continuous
8	2	8	—		2	8	Solifluxed willow *mo*	Ash band distinct, but thrown into folds. Recolonized terraces
9	—			7	—		Solifluxed willow *mo*	Ash band broken in many places
10	—			10½	—		*Salix herbacea*, closed stage	Soil exceeding 2 ft. in depth. Ash band very imperfect
11	4	6	—		—		*Salix lanata* invading *S. herbacea* mat	No ash band. A covering of silt and humus from 5 in. to 11 in. deep lies over gravel
12		10	—		1	11	Solifluxed willow *mo*	10 in. of peaty soil lying over silt
13	2	2	—		2	6	*Myri*	No shingle obtainable. 17 in. of peaty soil lying over silt
14	1	0	—		2	2	*Myri*	No shingle. 15 in. of peaty soil over silt
15	1	8	—		2	4	*Myri*	No shingle. 15 in. of peaty soil over silt
16	1	10	—		1	10	*Myri*	No shingle. 12 in. of peaty soil over silt

a survey of this piece of land, showing the different plant communities. At first sight there appear to be only two major plant communities: a bog at the side of the river with moss hummocks and frequent open pans of water, and on the hillside, away from the river, a dry area dominated by dwarf willow and other small shrubs. This willow community gradually becomes sparser, till at a height of about 2200 ft. (670 m.) it gives place to the impoverished open vegetation of the screes. On closer inspection, however, the vegetation is seen to consist of a greater number of types, varying according to their edaphic and physiographic situations. These are:

(*a*) The marsh (*myri* and *floi* of Hansen).

(*b*) The stream fans in various stages of colonization.

(*c*) The willow community of the hillside (*mo* of Hansen).

(*d*) The willow community at the bottom of the hillside, where the water table is within 6 in. of the soil level in summer and there is well-marked frost heaving (knolly *mo* of Hansen).

(*e*) Late snow-covered areas (*geiri* of Hansen).

(*f*) Areas with a snow cover shorter than that of (*e*), but longer than that of (*c*), where *Salix herbacea* forms a close and almost exclusive community.

(*g*) Stream banks.

(*h*) Open communities such as those of rock outcrops, hilltops and screes.

(*a*) Myri

The marsh community or *myri* extends from the river-bank to the colonized stream fan into which it imperceptibly merges. The *myri* is true tundra, mosses being the characteristic plants and phanerogams entirely subordinate, and as in all true tundra the subsoil is frozen even in August at a depth of only 2 ft. The appearance varies little: occasional pans of open water lie among an expanse of spongy moss hummocks, arranged irregularly but usually closely packed together. The hummocks are usually circular, about 18 in. (45 cm.) across and 9 in. (23 cm.) high; they are composed entirely of moss and the dead remains of moss. The depressions between the hummocks either coincide in height with the water table or are just above or below it. On the tops of the hummocks the following phanerogams are present:

Calamagrostis neglecta	a.	Polygonum viviparum	a.
Deschampsia alpina	a.	Salix lanata	o.
Carex Goodenoughii	a.	S. phylicifolia	o.
C. rariflora	a.		

In the depressions between the hummocks *Cardamine pratensis* and *Comarum palustre* occur irregularly.

The zonation of mosses in the *myri* is well defined and appears to be governed primarily by the height of the habitat above the water table. A characteristic transect together with the soil water *p*H (as determined by a B.D.H. capillator set) is shown in Fig. 1. In this diagram it will be seen that the tops of the highest hummocks away from the running water have a covering of *Sphagnum teres* with a layer of *Camptothecium nitens*, *Paludella squarrosa* and *Calliergon stramineum* beneath. The *Sphagnum teres* layer does not extend far down into the centre of the hummock, but grows on the dead remains of the moss layer below it. It will also be seen from the diagram that there is a very sudden change in *p*H values from the river water, 7·8, through the water in the *Drepanocladus uncinnatus* layer, which surrounds the hummocks, at 7·5, to the water in the *Sphagnum* layer at 6·6. From this it appears that the hummocks have been built up by a succession leading from the more alkali-tolerant species to the less alkali-tolerant. These moss hummocks are therefore quite different in origin from the soil hummocks in the *jaður* which are the result of frost action.

In the survey of the special area (Map 3) numerous pans of open water are shown in the *myri*. They are fringed normally with cotton grasses (*Eriophorum Scheuchzeri* and *E. polystachion*), though round the deeper ones there may be an inner layer of *Carex Lyngbyei* and *C. rostrata*. No floating vegetation was observed in pans on the east of Snaefell, but in the pans on the west, which are deeper and probably of greater age, *Zannichellia palustris* was frequently recorded. The breadth of the pans seldom exceeds 10 yards, and the depth of water is rarely more than 18 in. (45 cm.). The origin of these pans was at first thought to be the silting up of drainage channels as in the salt marshes of the Dovey estuary described by Yapp & Johns (1917). A careful examination of their distribution, however, precludes such an explanation for all the pans, and the following suggestion is put forward for the origin of certain ones. In the largest pan in the survey, through which a stream runs, there is a low island (in the middle of which is pit no. 12). This island is shown in Pl. 1, phot. 1; it is surrounded by a complete channel of water which does not exceed 18 in. (45 cm.) in depth. The outer edge of the channel is normal in all respects, with a fringe of cotton grass and the usual mosses: the inner edge, however, is quite abnormal, as the island itself, though it only rises 18 in. (45 cm.) above the water-level, does not belong to the *myri* formation, but to the solifluxed type of willow scrub, which would be normal on the screes, but is entirely unexpected here. The contrast between the outer and inner margins of the

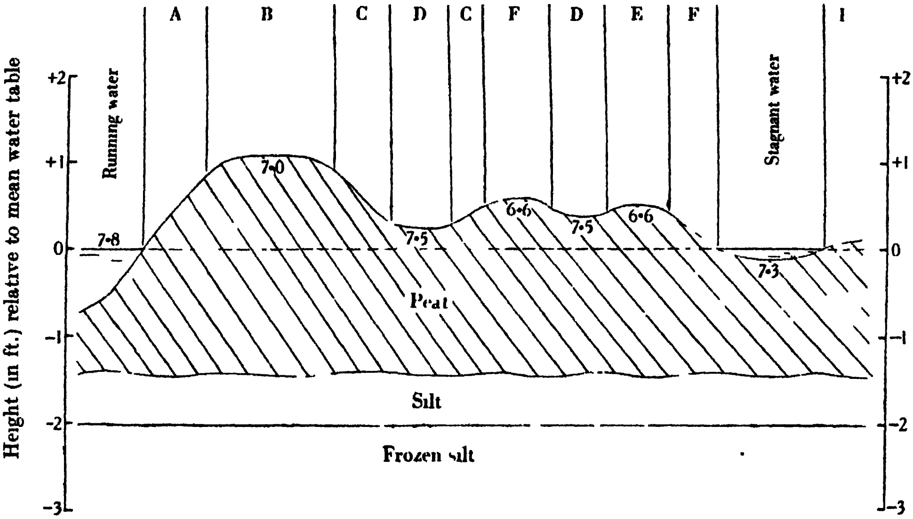


Fig. 1. Diagrammatic section through *Myri* to show vertical distribution of mosses. The numbers represent *p*H values. The horizontal scale is the same as the vertical. A, *Philonotis* sp.; B, *Mnium affine*; C, *Camptothecium nitens*, *Paludella squarrosa*, *Calliergon stramineum*; D, *Drepanocladus exannulatus*; E, *Sphagnum teres* (*Climacium dendroides*, *Mnium affine*); F, *Calliergon stramineum*.

channel is thus excellently marked, for on the outer edge there is the normal layer of cotton grass while on the inner the dwarf willows, *Cassiope* and *Empetrum*, heavily breached as described on p. 14, run right down to the water-level and actually extend below it. From this contrast it is clear that the outer margin of the channel is a relatively old and permanent structure, while the inner margin and the whole island are in an unstable state, turf breaching breaking up the surface of the island and rapidly lowering it in height through pushing the vegetation outwards into the surrounding channel. This conclusion is further strengthened, since not only does the breached vegetation extend beneath the water-level, but even in the deepest parts of the channel half-submerged dead willow roots are to be found. Further exploration of the pans revealed the fact that this was not an isolated case, for in three pans where no islands existed, willow roots could be found submerged in the silt, while there was, as usual, no willow in the cotton-grass verge. In two other cases, also at the edge of pans, a low hummock was being broken up by turf breaching and slowly pushed into the open water.

From these facts it appears that the origin of some of the pans is intimately connected with the origin of the whole *myri* system, and to investigate this more thoroughly a series of diggings was made. This was difficult since the diggings were entirely below the water table, and it was impossible to dig deeper than 2 ft. since the soil was always frozen at that level. The diggings, however, showed that the greatest depth of moss remains was only 17 in., and that below that level (which varied in all only 4 in.) the *myri* rested on pure silt, such as forms much of the bed of the Jökulsá i Fljotsdal. In none of the diggings was there any sign of the white ash band. The following very tentative hypothesis is therefore put forward to account for the origin of the *myri* formation. An original substratum for colonization was provided by the silt deposited either by the Jökulsá i Fljotsdal itself or more likely by its tributaries from the eastern slopes of Snaefell. Such bare patches are to be seen frequently to-day; they are by no means level, since the original sandbanks persist as mounds above the level of the river bed. On the lower parts of this substratum colonization by mosses would have led up to the type of succession taking place in the marsh to-day. Drainage channels from the streams coming down the mountain side would have silted up or been blocked by the encroaching vegetation, and some of the pans would thus have been formed. While this was happening on the lower ground, a different type of succession would have taken place on the mounds, and since they would have stood considerably above the water table the succession on them probably resembled that taking place at present on the screes and river fans, and led to the typical dwarf willow stage. In such an exposed position this could not be stable, and turf breaching would set in, gradually lowering the height of the mounds. Two processes would then have been at work; the mounds were gradually being lowered and the marsh was gradually rising through the

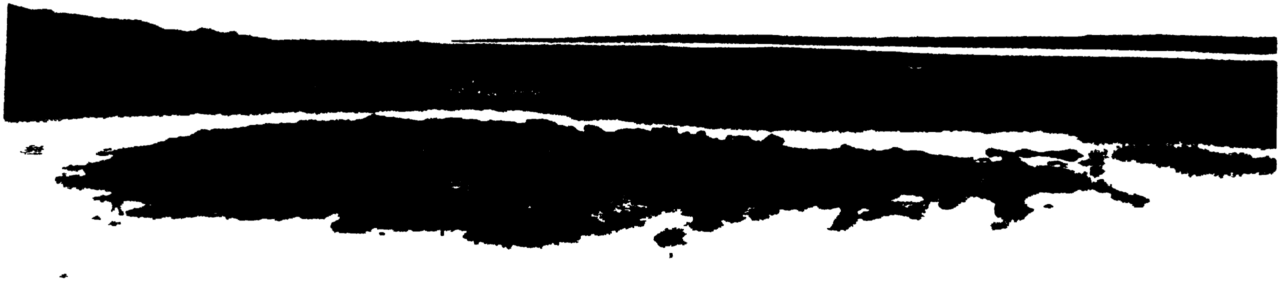


Photo 1. The sinking island. Turf breaching is clearly visible, the vegetation being gradually pushed into the surrounding channel. Note the stable outer edge of the channel.

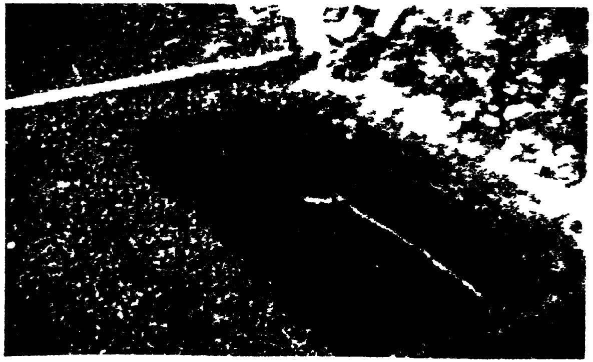


Photo 2. Pit No. [illegible] in *Salix herbacea* mat. The ash band is level and continuous, showing that no solifluxion has taken place.

Photo 3. Pit No. [illegible] S. Ash band showing signs of disturbance of the surface. The vegetation is dense but the ground is terraced and recolonization has followed step formation.

accumulation of moss remains, and so raising the water table with it. If these two processes continued steadily, the paradoxical stage would be reached where the original mounds had been converted into pans of water surrounded by moss hummocks formed from the succession on the originally lower ground. No other hypothesis at present seems more satisfactory than this, but it cannot be claimed that even this is entirely satisfactory, since no evidence from other places is available to show the exact course of colonization on a freshly exposed silt river bed.

The total absence of the ash band from any part of the *myri* has two possible explanations. Either the ash was deposited on the *myri* at a time when colonization by plants had proceeded to a certain degree and the ash was then removed by floods before further plant growth could bury it, or more likely, the whole development of the *myri* system is comparatively recent and has taken place since the ash deposit. In the latter case the area now occupied by *myri* would either have been river bed or bare silt, and ash could scarcely be expected to remain on these. In the former case, some trace of ash would be expected, and the latter supposition is therefore probably correct.

(*b*) *Colonized stream fans* (jaður *and* mo)

In the area chosen for detailed examination, the only stream which drains the hillside appears to have been much greater in former times than it is now, and though it has deposited a considerable gravel fan, there is no evidence to show that it has altered its course recently. Consequently, the fan is in an advanced state of colonization, and even where it stands highest above the water table there is a deposit of 5 in. (13 cm.) of soil above the shingle. Nearer the river the depth of soil above the shingle increases, and the water table rises relative to the surface; thus at pit 11 the shingle is 5 in. (13 cm.) below the surface, and the water table 4 ft. 6 in. (1·4 m.), while at pit 13 no shingle can be obtained since soil extends down to a depth of 2 ft. 6 in. (0·76 m.) below the surface, and the water table also stands at that level. On the river side, therefore, the fan vegetation merges imperceptibly into the marsh, but on the side away from the river it is sharply demarcated by a steep bank at the end of the scree. The vegetation of the fan in its drier part consists of

Salix lanata	a.	**Silene acaulis**	o.
S. phylicifolia	a.	**Thalictrum alpinum**	o.
S. herbacea	a.	**Vaccinium uliginosum**	r.
Cassiope tetragona	a.	**Pedicularis flammea**	r.
Empetrum hermaphroditum	a.	**Equisetum arvense**	o.
Juncus trifidius	o.		
Poa alpina, var. vivipara	o.	**Aulacomnium palustre**	
Carex rigida	o.	**Dichodontium pellucidum**	
Rumex acetosa	o.	**Rhacomitrium ramulosum**	
Luzula spicata	o.	**Drepanocladus uncinnatus**	
Deschampsia alpina	o.	**Mniobryum albicans**	
Euphrasia frigida	o.	**Camptothecium nitens**	
Armeria maritima	o.	**Cynodontium virens**	
Tofieldia palustris	o.	**Splachnum vasculosum**	

Comparisons with other fans show that this vegetation is characteristic of a late stage in the succession. By comparing different fans and also by comparing different parts of the same fan, it is possible to deduce the course of the succession with some certainty. When a stream swings across its fan it leaves behind it an area of bare, damp gravel usually with low ridges. The first colonist is the moss, *Rhacomitrium ramulosum*, which fills the spaces between the stones in the hollows and later covers the stones themselves. The thick cushions thus formed retain a large quantity of blown sand and thereby form a nidus for the next arrival, *Salix herbacea*. An area of fan that has recently been exposed bears a large number of rapidly increasing cushions of this type in the hollows, and both components play an important part. *Salix herbacea* seems unable to colonize bare ground, while *Rhacomitrium ramulosum*, if its cushions exceed a certain size without further colonization, is destroyed since its centre dies and a small blow-out starts, which ultimately extends to the whole cushion. Before the cushions join together other colonists arrive; the most frequent of these are *Silene acaulis*, *Armeria maritima*, and *Polygonum viviparum*. It is noteworthy that the two former may colonize bare ground, but when they do so their presence does not lead to further colonization, since their cushions are too dense to afford a foothold to other plants. When finally the cushions in the hollows join, a close *Salix herbacea* mat is formed, and as the soil level in the hollow rises, colonization on the ridges proceeds, but is usually not completed without invasion from the hollows at the sides. From the *S. herbacea* mat stage the succession may proceed along at least two lines. On the lower part of the fan, near the *myri*, the more hydrophilous mosses succeed the initial *Rhacomitrium ramulosum*, and a phanerogamic flora resembling that of the *myri* is developed, while on the higher parts the flora given above replaces the original *Salix herbacea*, the first arrival being *S. lanata*, closely followed by *Cassiope tetragona*. Probably the final stage is reached when *Salix lanata* becomes dominant, but this was never found, since the course of events at any rate on the fan of an active stream appears to be cyclic. In the case of the fan of a stream south of the special area, the vegetation had almost reached this final stage, but the stream was swinging back rapidly and cutting away the bank, so that the vegetation was being destroyed. It is interesting that the vegetation, which was thus being destroyed, had already suffered severely from wind erosion, nothing being left but the willows themselves, and their dead remains. Such severe wind erosion does not occur elsewhere in the Snaefell area, and it seems likely that the first erosion is due to the stream and that this then provides means for the wind to destroy the ground vegetation, which is normally covered by the prostrate stems of the willow. When the ground vegetation has been destroyed, the willow roots are soon exposed, and this in turn brings about their death.

The soil profile exposed by the undercutting of the bank of this active stream mentioned above is of some interest. The bank is approximately 4 ft. (1·3 m.) above the stream level. The whole of this bank is composed of a very sandy soil with varying degrees of humus in it, except for the lowest 6 in., which is entirely gravel. The stream is therefore removing all the soil which has accumulated as well as 6 in. of gravel which it had deposited at an earlier date. As is to be expected, no large stones are to be found in the soil, though there are occasional deposits of small ones, presumably brought down by floods. The white ash band shows particularly clearly and appears in profile as a sinuous line, about 1½ in. (4 cm.) thick, and with a mean depth below the surface of 22 in. (55 cm.). If the date of the deposit of the ash band was known, it would therefore be possible to make an approximate calculation of the time taken for the complete cycle of events to occur.

(c) *Willow community of the hillside* (mo)

The willow community of the hillsides closely resembles the willow community found on the shingle fans, and if the development of the latter could proceed indefinitely the two vegetations might in time be identical. Succession on the shingle fans, however, always appears to be terminated by the swinging back of the stream, which in the first instance deposited the shingle, whereas succession on the most favoured part of the hillside leads to what at least appears to be a climatic climax. Where the willow community is best developed it consists of a three-layered system growing on at least 4 ft. (1·3 m.) of soil, the lower part of which consists of a fine sand of weathered basalt, while the upper 18 in. (50 cm.) has added to this a varying proportion of humus. The three layers consist of a diffuse canopy formed by the willows and other taller shrubs about 18 in. (50 cm.) high; a herb layer below this, and on the ground-level a dense covering of mosses and such dwarf shrubs as *Empetrum hermaphroditum* and *Cassiope tetragona*, which together form a compact covering round the stems of the taller shrubs. The following plants occur throughout the willow community:

Salix lanata	l.d.	Viscaria alpina	o.
S. glauca	l.d.	Galium silvestre	o.
S. phylicifolia	l.d.	Dryas octopetala	o.
Empetrum hermaphroditum	f.	Luzula spicata	o.
Vaccinium myrtillus	f.	Armeria maritima	o.
Salix herbacea	f.	Silene acaulis	o.
Loisleuria procumbens	f.	Kobresia Bellardi	o.
Poa alpina var. vivipara	f.	Betula nana	r.
Cerastium alpinum	f.	Gentiana nivalis	r.
Cassiope tetragona	a.	G. tenella	r.
Polygonum viviparum	a.	Veronica alpina	r.
Thymus serpyllum	a.	V. fruticans	r.
Bartsia alpina	o.	Equisetum arvense	o.
Pedicularis flammea	o.	Botrychium lunaria	r.
Euphrasia frigida	o.	Selaginella selaginoides	r.
Thalictrum alpinum	o.		
Potentilla verna	o.	Dichodontium pellucidum	
Erigeron uniflorus	o.	Cynodontium virens	
Gnaphalium supinum	o.	Drepanocladus uncinnatus	
Tofieldia borealis	o.	Rhacomitrium ramulosum	
Carex rigida	o.	Polytrichum juniperinum	

On the hillside east of Snaefell only a single plant of *Betula nana* was found, though further north in similar positions and only 300 ft. (90 m.) lower, and further west near the Jökulsá á Bru at an altitude of 1900 ft. (580 m.), this is the dominant shrub. In the west of Iceland, *Betula nana* has a very sudden upper limit to its vertical distribution, and its almost complete absence from the Snaefell district appears to be due to the altitude and corresponding severity in climate. This is of interest since it has often been observed (e.g. Thoroddsen, 1914, p. 299) that the Icelandic flora is in general indifferent to altitude, and considerable difficulty must attend the problem of inferring climatic conditions from plant remains. When this problem is undertaken, *Betula nana* will, therefore, be a significant indicator. Another plant not occurring in the Snaefell area, apparently on account of altitude, rather surprisingly is *Alchemilla alpina*, the upper limit of which occurs slightly above that of *Betula nana.*

In moist places, where the water table approaches within 18 in. (50 cm.) of the soil level, in addition to the species listed above, there are also to be found:

Carex Goodenoughii
Juncus balticus
Rumex acetosa
Sibbaldia procumbens

together with the more alkali-tolerant mosses of the *myri.* In still moister hollows on the hillside, where the water table lies almost at soil-level, the shrubs are absent and the normal herbs are replaced by *Eriophorum polystachium, E. Scheuchzeri* and *Juncus balticus*, with such mosses as *Calliergon stramineum* and *Drepanocladus exannulatus.*

Although the willow community of the hillside appears the most luxuriant type of vegetation found in the area, containing the greatest density of plant species as well as the greatest number of species, its continuity is by no means certain, since it is liable to severe erosion by solifluxion and wind action. High up on the hillside solifluxion may be seen in action even in July and August. An upper layer of scree, 3 or 4 in. deep, slides over a deeper frozen layer, the water and fine particles in the upper layer acting as a lubricant to facilitate the movement of the larger stones. The geomorphological aspect of this has been studied in detail by W. V. Lewis, and the effect of such solifluxion on plant life will be discussed later. On the lower parts of the hillside, where there may be a comparatively dense covering of vegetation growing in the type of soil described above, solifluxion can hardly be such a simple phenomenon, but that it takes place can readily be seen from the soil profile in Pl. 1, phot. 3. Even in thickly vegetated areas, therefore, where no large stones are to be found except on the surface or below a depth of 7 or 8 ft., solifluxion must occur. An examination of the root systems in the willow community shows that those of the larger shrubs may extend 4 or 5 ft. (1·2–1·5 m.) vertically into the soil, and there is no doubt that movement of the soil in solifluxion does not extend to such a depth. Consequently, the effect of solifluxion is to break the roots of the larger shrubs, causing rifts to occur in the vegetation covering. It is impossible to tell how large these rifts might become if solifluxion were the only eroding agent, for once a rift is formed two other agents operate and their action is more violent than that of solifluxion. In the first place, snow collecting in a rift will freeze and expand, thus increasing the original rift (cf. Nansen, 1912). Secondly, when a rift has once been established, wind erosion will rapidly enlarge the original rift by removing the moss layer round the stems of the shrubs and subsequently lay bare the roots of all but the largest shrubs. Wind erosion of this type, though less rapid on the pre-glacial basalts of the Snaefell area than on the post-glacial lavas farther west, can be seen in action on any dry, windy day in summer.

The effects of these agents of erosion can be seen almost throughout the willow community on the hillside. Instead of bearing the uniform covering of vegetation described above, the hillside is thrown into terraces or steps (Pl. 2, phot. 6). The tread of the step is a horizontal area of varying breadth, almost denuded of plant life; the vertical edge, which varies between 2 and 6 in. in height, is thickly vegetated and rises slightly above the level of the horizontal area behind it, so that a rim is formed. On the inner side of this rim there are a large number of broken roots and others which have been dragged up from the soil of the horizontal area behind the rim; these demonstrate clearly that the vegetation of the vertical area once grew on the horizontal part behind it, but has now been forced downhill, presumably by expansion on freezing of moisture held in the saucer-shaped step above.

In the survey of the special area, the solifluxed areas of the willow community were carefully distinguished from the areas where no solifluxion had taken place, and since this alone was not sufficient to explain why certain areas were free from solifluxion and terracing, a series of levels was undertaken, giving the gradients along a typical sector from the river to a height of 450 ft. (100 m.) on the hillside above it. The survey and sector together showed that there is surprisingly little correlation between solifluxion and gradient. For example, around the camp where the gradient is only 1 in 15, the soil has been almost completely denuded by solifluxion and the accompanying agents of erosion, while higher up on the slope, with a gradient of 1 in 5, there is a dense covering of the normal willow community. There is, however, a partial correlation between the presence of solifluxion and the proximity of rock outcrops and it seems legitimate to conclude that a more important factor than gradient is depth of soil. From the survey it will be seen that in the neighbourhood of outcropping rock, solifluxion has always taken place, and the one undisturbed area in the survey is that furthest removed from outcrops above or below it. On the other hand, in the area round the camp the soil certainly exceeded 8 ft. (2·4 m.) in depth, as shown by the section cut by the stream near it, and it can only be concluded, therefore, that all the factors controlling solifluxion are not known.

In many cases it is likely that solifluction and the accompanying terracing deflect the course of plant succession, but do not indefinitely retard it, for though large areas of soil are denuded, recolonization occurs slowly and in many places where the soil was thrown into terraces, these had the normal close covering of vegetation. The deflected succession was not worked out in full, but the following steps seem to be general. *Equisetum arvense* is the pioneer on the bare terrace and its rhizome system starts to bind the soil, the binding being helped by the arrival of such mosses as *Dichodontium pellucidum* and *Drepanocladus uncinnatus*. After this come *Polygonum viviparum* and *Salix herbacea*, the latter rapidly becoming dominant and yielding place only when the covering is complete to *S. lanata* and the usual components of the willow community.

In its floristic composition, the typical willow community described above conforms to none of Hansen's types, and this is not altogether surprising since though it occurs with some regularity throughout Iceland, it is only found above the highest limit at which Hansen worked. The species list on p. 13 shows that the community approximates very closely to the *Betula nana mo* of Hansen (1930, p. 103) and differs only in that *Betula nana* is replaced as the dominant form by the three species of *Salix*. The significance of this has already been discussed on p. 14, where it is suggested that the absence of *Betula nana* is an effect of increasing altitude. On account of the general resemblance of the two communities and of their environmental conditions the name *Salix mo* or willow *mo* seems applicable for the type of willow community described on p. 13, and it is therefore referred to by this name throughout the rest of this paper.

(*d*) *Knolly* mo

In one part of the special area, where the hillside merged with the level of the *myri* without any intervening rock outcrops, a highly modified type of willow community was found, bordering on its lower side on *myri*, on another passing quite suddenly into the willow scrub of a recolonized stream fan, while elsewhere it merged into willow *mo* on the screes. In this area the water table is within 1 ft. (30 cm.) of soil-level and flooding was frequent. The characteristic feature of the area is the small knolls, having the same size, shape and distribution as the hummocks in the *myri*, but with a different origin and structure. Each knoll is composed entirely of soil and its origin is undoubtedly due in some way to frost action. No detailed excavations of the knolls were made, but a full description of their structure and possible origin is given by Thoroddsen (1914, p. 262 et seq.). The knolls he investigated consisted of a kernel of clay surrounded by a layer of humus and plant remains. The knolls are said to be increased in size by the upward flow of the clay and as evidence of this he cites ash bands which become bent upwards by the rising clay. The mechanism of the upward flow is complicated and is ascribed to evaporation

Phot. 4. Knolly *mo*. Between the hummocks the most conspicuous plants are *Hieracium petiolosum*. The ruler is 1 foot (*ca*. 30 cm.) long.

Phot. 5. Recolonized terraces with close willow *mo*.

Phot. 6. Severe turf breaching on a gradient of 1 in 30. The dead willow roots pulled out of the ground can be seen behind the broken edges of the turf.

Phot. 7. Terrace formation on scree, caused by solifluxion.

from the knoll during the day with a consequent upward rise of water, followed by freezing and expansion of the water at night and alternate thawing and contraction by day. This series of events is said to give rise to a process of soil sorting by which the smaller particles are moved upwards and the larger particles left behind or pushed to the side. Since no detailed investigations were made at Snaefell it is impossible to say how far Thoroddsen's explanation holds good for the knolls there; his statement, however, that knolls are formed only in places with poor drainage and no spring snow cover is of interest from the point of view of the vegetation. At Snaefell the physical conditions necessary for knoll formation to take place appear to resemble those recorded at Arnavatnsheiði by Hansen (1930, p. 106), viz. a snow cover intermediate between that of willow *mo* and *geiri* and a water table intermediate in position between that of *mo* and that of *myri*.

The vegetation differs considerably from that of willow *mo*: dwarf shrubs are less conspicuous and sedges and grasses predominate. In a typical area the following were present:

Carex rigida	a.	Thalictrum alpinum	o.
C. rariflora	a.	Poa alpina	o.
Deschampsia alpina	a.	Euphrasia frigida	o.
Calamagrostis neglecta	a.	Tofieldia palustris	o.
Hieracium petiolosum	a.	Pedicularis flammea	o.
Polygonum viviparum	a.	Silene acaulis	o.
Luzula spicata	a.	Armeria maritima	o.
Juncus trifidius	a.		
Salix glauca	f.	Aulacomnium palustre	
S. lanata	f.	Dichodontium pellucidum	
S. herbacea	f.	Drepanocladus uncinnatus	
Empetrum hermaphroditum	f.	Mniobryum albicans, var. glaciale	
Cassiope tetragona	f.		
Saxifraga hirculus	f.	Peltigera aphthosa	

Saxifraga hirculus grows only on the tops of the knolls, and by its regularity in that position serves to distinguish them from the adjoining moss hummocks in the *myri* where it is never found. This highly modified type of the willow community is well known throughout Iceland and is the "knolly *mo*" of Hansen (1930, p. 106).

(*e*) *Late snow-covered areas* (geiri)

The effect of prolonged snow cover in arctic regions is well known, and gives rise in Iceland to a type of vegetation known as *geiri*. *Geiri* occurs in the Snaefell district at altitudes not much above that of the river wherever a bank facing south or east gives shelter for snowdrifts to persist until about early June. The snowdrifts which thus persist in hollows or in between level and sloping ground shelter the plants beneath them from the cold of late spring and early summer, when hard frosts and strong winds are frequent. In addition, since *geiri* is always developed under banks and in hollows, the perpetual moisture may be beneficial in the very rare droughts. The *geiri* of the Snaefell district is similar to that in other parts of Iceland (cf. Hansen, 1930,

p. 114). The vegetation of three patches includes the following, all with a high degree of constancy:

Geranium sylvestris	l.d.	Salix glauca	o.
Alchemilla glomerulans	l.d.	Taraxacum devians	o.
Pyrola minor	a.	Hieracium petiolosum	o.
Alchemilla minor	a.	Gentiana nivalis	o.
Phleum alpinum	a.	Veronica alpina	o.
Ranunculus acris	a.	V. fruticans	o.
Salix herbacea	a.	Poa alpina	o.
Sibbaldia procumbens	f.	Thalictrum alpinum	o.
Erigeron uniflorus	f.	Polygonum viviparum	o.
Gnaphalium supinum	f.	Rumex acetosa	o.
Equisetum arvense	f.		

Mosses are almost entirely absent from this community, their place being partly taken by *Salix herbacea*. In the dampest places the liverworts *Marchantia polymorpha* and *Preissia quadrata* were occasionally present.

As Hansen has pointed out, the *geiri* has the highest proportion of plants with a restricted northern distribution of all the Icelandic types of vegetation, and this is doubtless due to the protection from extreme cold and desiccating winds afforded by the prolonged snow cover. It should, however, be noted that larger hollows and those at only a slightly greater altitude instead of being a favourable site for plant growth are particularly unfavourable, since in them the snow cover may linger till mid-July, and the season for growth is thus so restricted that practically no plant life occurs at all. An example of this is given on p. 23.

(*f*) Salix herbacea *mat*

Interspersed throughout the willow community of the hillside there occur small areas where *Salix herbacea* forms a thick and almost pure mat. One of these patches in the special area is shown in Map 3, where it occurs between the normal willow community and a stream gulley, at a height of 2200 ft. (670 m.). There is no terracing, although the gradient exceeds 1 in 20, and the smoothness of the mat is only disturbed by occasional tussocks of *Poa alpina* var. *vivipara*. In addition to the two species already mentioned, the following also occur:

Equisetum arvense	o.	Cassiope tetragona	r.
Sibbaldia procumbens	r.	Carex rigida (very stunted)	r.
Polygonum viviparum	r.	Rumex acetosa	r.

This community, as well as occurring occasionally throughout the willow community, is also found occupying a small belt below the *geiri* and in many places in shallow stream gullies above the general level of the willow community. A similar community, but differing in that it is never found covering the soil closely, is found on the horizontal part of the terraces where recolonization is occurring. For this reason it was at first thought that the *Salix herbacea* mat also formed a stage in recolonization of eroded areas. This hypothesis had to be abandoned when it was discovered that the *S. herbacea* mat was found only in undisturbed areas where there was no reason to suppose that recolonization was taking place. A soil profile 10 ft. (3 m.) in length cut through the *S. herbacea* mat at an altitude of 667 m. (part of which is shown in Pl. 1, phot. 2) revealed an unbroken, uniform white band 13 in. (35 cm.) below the surface, showing clearly that no solifluxion had taken place in that area, though it had been extremely active in the willow community bordering on it. Four other diggings in different areas established the same fact, in each case the white band being present and undisturbed at depths varying from 13 in. (35 cm.) to 5½ in. (14 cm.) below the soil surface. In the latter digging, which was on the west of Snaefell at an altitude of 2710 ft. (820 m.), besides the usual constituents of the *Salix herbacea* community, a few plants of *S. glauca* and *Saxifraga groenlandica* were present. In addition to establishing the fact that the *Salix herbacca* mat is found in undisturbed ground, the diggings also exclude the height of the water table as a factor determining the presence of the mat. In the first example, the water table stood 34 in. (0·85 m.) below the soil surface, and in the other cases it was still deeper than this, and since the normal willow community is developed on soils with both shallower and deeper water tables, this factor is therefore excluded from directly determining the presence of the mat.

The elimination of solifluxion and the available water supply as factors deflecting or delaying the normal course of succession leaves only physiographic or edaphic factors as the possible agents. Edaphic differences between the willow community and the *S. herbacea* mat are unlikely, as the two soils not only look very similar, but also come into direct contact, and there is no reason to suppose that sudden changes occur in the position or nature of the underlying rock. Physiographic differences also at first sight seem unlikely, since the two communities are often adjacent on slopes with similar gradients and aspects, but in the case of the *S. herbacea* mat occurring below the *geiri* and by the sides of gulleys above the normal level of the willow community, it is clear that the snow cover must be unusually long, since the drifts in the adjacent hollows will extend outwards and prolong the snow cover on the level areas at their sides. It is possible that the same, too, may apply to the only considerable area of *S. herbacea* mat in Map 3, since it is bounded on the north by a deep gully towards which it has a gentle slope, and the snowdrift accumulating in this may well extend farther than in places where the gully has steeper sides. It is therefore suggested that *S. herbacea* mat is formed by a deflected succession from that giving rise to the normal willow community and is caused by a snow cover intermediate in duration between that of the *geiri* and that of the sterile snow patches described on p. 23. This hypothesis could not be checked directly since our observations started only at the beginning of July when the lower parts of the hillside were already free from snow. The fact, however, that areas of *S. herbacea* mat have never been subject to solifluxion, strongly suggests that they have an abnormally long snow cover, since on the gradients and in the positions they occur solifluxion would be expected, and its absence suggests that there must be some cause inhibiting it. The only factor that would totally inhibit solifluxion, apart from a very dense covering of vegetation, is prolonged snow cover, since this prevents the exposure of the ground at a time when intense cold is to be expected.

(*g*) *Stream banks*

Where a considerable depth of soil exists on the hillside, the streams cut gullies which may be as much as 7 ft. (2 m.) deep. Meandering of the streams is always taking place, and consequently one bank of the gully is usually being eroded while the other is stable and affords a suitable site for plant colonization. In general, the vegetation of the stream banks bears a resemblance to *geiri*, since the gullies are protected by a snow cover persisting through the early summer, but whereas *geiri* occurs in well-drained positions with an approximately southern aspect, the stream banks are very moist and usually sheltered from direct sunlight except for a short period. Consequently such plants as *Geranium sylvestris* and *Pyrola minor* are absent from the stream banks except in shallow gullies where the stable bank has a southern aspect.

The characteristic vegetation of the steep part of a stream bank is made up of the following species:

Salix herbacea	a.
Sibbaldia procumbens	f.
Cassiope tetragona	f.
Cerastium alpinum	f.
Sagina procumbens	f.
Polygonum viviparum	f.
Equisetum arvense	f.
Alchemilla minor	o.
Ranunculus acris	o.
Thalictrum alpinum	o.
Armeria maritima	o.
Silene acaulis	o.
Euphrasia frigida	o.
Carex Goodenoughii	o.
Phleum alpinum	o.
Gnaphalium supinum	o.
Erigeron uniflorus	o.
Gentiana nivalis	r.
Taraxacum devians	r.

together with the mosses *Webera cruda* and *Desmatodon latifolius*. The transition to this vegetation from the willow community is marked by the loss of all the larger shrubs. The vegetation on the stream bank is close but has two layers only. Often the stream bank becomes flatter near the stream, and below the steep bank described above there may be an almost level area 4 or 5 ft. across. This level area is much damper than the steep side of the gully and contains certain hydrophytic species which are otherwise only found on the moist higher parts of the screes below melting snow patches. The following species occur (arranged in the order of a typical transect from the steep part of the bank up to the margin of the stream):

Phleum alpinum
Eriophorum Scheuchzeri
Saxifraga stellaris
Alsine rubella
Sagina Linnaei
Ranunculus pygmaeus
Cerastium fontanum
Epilobium Hornemanni

and the bryophytes *Drepanocladus uncinnatus*, *Philonotis tomentella*, *Mniobryum albicans*, and *Marchantia polymorpha*. At a height of about 400 ft.

(120 m.) above the river, where there is no depth of soil, the gullies formed by the streams become shallower and there is no sharp distinction between the sides and the floor of the gully. The vegetation of the banks is impoverished, but two further species occur: *Saxifraga rivularis*, growing near the water's edge, and higher up the streams *Arabis alpina*, which at this level grows only near running water. Not far above this region the streams rise, and above that level all drainage is by underground seepage.

(*h*) *Rock outcrops, screes and hilltops*

These three situations differ from the areas so far described and resemble each other in that they support open communities of vegetation where colonization and regression can be recognized with a high degree of certainty. This is important, since a clue is thus provided to the early stages of colonization elsewhere.

In Map 3 it will be seen that there are large areas of rock outcrop at the bottom of the hillside. These outcrops take the form of slabs and blocks with numerous cracks suitable for plant growth. The moss, *Rhacomitrium canescens*, appears to be the first colonist in these cracks, filling them completely and providing a supply of humus for the vascular plants which follow; these are:

Salix herbacea
Dryas octopetala
Poa alpina
Thymus serpyllum
Galium sylvestre
Kobresia Bellardi
Botrychium lunaria

None of these succeed in forming a thick covering over the rocks, and only the stems of *Dryas octopetala* extend far from the original crack. In addition to the plants already mentioned, *Saxifraga oppositifolia* and the lichens, *Usnea melanoxantha*, *Gyrophora cylindrica*. *Rhizocarpon geographicum*, *Umbilicaria erosa*, *Alectoria pubescens*, *Stereocaulon denudatum*, are also found in moderate quantities. *Saxifraga oppositifolia* does not seem to make use of cracks already occupied by moss, though it may need the small quantity of humus that is provided in fissures where lichens have been attached. Neither the first type of colonization started by *Rhacomitrium canescens*, nor the second started by the lichens appears to lead far. In the first case, this is the result of the absence of mosses which are able to spread over the bare areas of rock intervening between the fissures. Phanerogams, apart from *Saxifraga oppositifolia,* are unable to colonize the bare rock surface, and consequently no closed community can be formed until the rock is broken by frost action into scree. In the second case, the lichen covering is never permanent enough for further colonization, and this presumably is partly the result of the relatively rapid weathering of the rock surface at such a high altitude, and partly of the reduced rate of growth of the lichens as compared with that at sea-level. The rock outcrops seem to indicate, therefore, that nothing approaching the normal willow community can be formed on soil directly developed on bare rock, until the rock is first reduced to scree.

The vegetation of the screes is of two moderately well-defined types. At the upper limit of the willow community with increasing height solifluxion becomes more and more severe, and the depth of soil consequently diminishes until eventually nothing but scree is found. With the disappearance of the soil, however, the vegetation does not cease abruptly and numerous members of the willow community persist for another 300 or 400 ft., struggling against the movement of the scree. The second type of scree vegetation is a more alpine type, occurring higher on the mountain side and including many species not found elsewhere in the area. These two types of scree vegetation will now be described.

In the typical willow community solifluxion gives rise to terraces with low, broad steps; in this case solifluxion probably causes only the initial breach, and an expanding pocket of frozen snow enlarges the breach so formed. At greater altitudes and with an increased gradient, solifluxion becomes more important. The frozen layer is nearer the surface and present far longer, and solifluxion can therefore proceed with greater violence, destroying plants before their roots can restrict its movement and thus preventing the formation of soil. In such conditions instead of terraces, only occasional plants occur. They hold up for a time the movement of the screes, but eventually become submerged beneath them. The majority of the plants occurring above the level of the terraces are those which are found most abundantly in the willow community, but with these are interspersed a few typically "scree" plants. The following compose the first type of scree vegetation, where solifluxion prevents even the formation of terraces, but where the frequency exceeds five plants per square metre. Those plants which are found in the moist areas only are marked with an asterisk:

Salix lanata	f.	Gnaphalium supinum	o.
S. phylicifolia	f.	*Epilobium alsinifolium	o.
S. herbacea	f.	Veronica alpina	o.
Poa alpina	f.	*Luzula spicata	o.
*Salix glauca	o.	Armeria maritima	o.
Sibbaldia procumbens	o.	Silene acaulis	o.
Euphrasia frigida	o.	Cerastium alpinum	o.
Cassiope tetragona	o.	Oxyria digyna	r.
Empetrum hermaphroditum	o.	Saxifraga groenlandica	r.
Saxifraga oppositifolia	o.	S. nivalis	r.
Dryas octopetala	o.	*Sedum roseum	r.
Thymus serpyllum	o.	*S. villosum	r.
Erigeron alpinum	o.	Arabis petraea	r.

The mosses already mentioned in the willow community also occur on the screes with the exception of *Polytrichum juniperinum*; there are, however, no additions to these.

In the special area, with increasing altitude acting probably through accelerated solifluxion, the vegetation described above becomes sparser and sparser and with the greater gradient above the 800 m. (3200 ft.) contour the vegetation ceases completely. Below this level, however, there is also an entirely bare patch of scree, between the 710 and 740 m. contours (Map 3).

This area when seen at a distance resembles some of the cotton grass patches through the shining appearance of the wet scree, of which it largely consists. The cause of the complete lack of vegetation here is undoubtedly the prolonged snow cover, since the whole area forms a hollow in which the snow lingers till mid-July, thus leaving too short a growing season for vegetation to develop. Many of the damp, bare gullies formed by old stream courses probably owe their lack of vegetation to the same cause.

The second type of scree vegetation differs from that already described in that it occurs higher on the mountain side, and that in it the total frequency of plants never exceeds five per square metre. It is typically found below snow patches and in other places where there is an abundant supply of moisture; it closely resembles the vegetation of the Swiss moraines. The most abundant species is *Ranunculus glacialis*, and in addition to it there occur occasional plants of:

Oxyria digyna
Sedum roseum
S. villosum
Arabis petraea
Draba alpina
Saxifraga groenlandica
S. nivalis

Where these occur, lichens and mosses are absent, and it is only on the dry parts of the screes, where there are large boulders, that these are present. On such boulders a vegetation resembling that of the rock outcrops is found, but without the phanerogams.

On the east of Snaefell no level areas of any size occur above the stream fans. On the west, however, there are large areas with only a slight gradient, and on these stone sorting occurs with a symmetrical arrangement of plants, which offers the nearest approach to that described by Polunin (1934) on Akpatok Island. The geomorphological aspect of this type of stone sorting has been described by W. V. Lewis and cannot be discussed in detail here; the following, however, is a brief summary of his views. At high altitudes (i.e. above about 800 m.), even on a gradient of as little as 1 in 30, solifluxion takes place. A mass of predominantly fine material sludges downhill, pushing to the sides the larger stones which are more difficult to move, thus giving rise to a partial sorting. The bands of larger stones form the natural means of surface drainage and channels develop. Since these larger stones in time become relatively stable and are continually moist, colonization by plants starts round them and they alone often are covered by vegetation while the area of smaller stones is left bare. In such cases the vegetation on and around the large stones consists of such hydrophilous mosses as *Philonotis fontana*, *Mniobryum albicans* and *Drepanocladus uncinnatus*. *Poa alpina*, *Salix herbacea* and *Cerastium alpinum* are also usually present. There is no evidence that colonization of this type ever proceeds further than this stage, and probably only an increase in the mean annual temperature with a consequent retardation of solifluxion could make further colonization possible. But clearly much of the colonization of land which has recently been uncovered by the retreat of glaciers must proceed in this way.

In the description of the Kverkfjöll district (Anderson & Falk, 1935), the vegetation of the hilltops formed a major division. This is not so in the Snaefell area since the pre-glacial lavas, which form the greater part of its rock, weather less rapidly than the post-glacial lavas of the Kverkfjöll district, and consequently form a more stable substratum for plant growth. In the latter area the only substratum which is both moderately stable and free from inundation by blown sand is the bare rock outcropping above the screes, and this, therefore, bears a vegetation which differs greatly from that of the valleys. Nevertheless, certain hilltops in the Snaefell area, where rock outcrops above scree, support an open type of vegetation closely resembling that of the hilltops in the Kverkfjöll district. In such places the vegetation is similar to that already described for rock outcrops at lower altitudes, but in addition to the species mentioned the following also occur:

Veronica alpina
Saxifraga nivalis
S. groenlandica
Gnaphalium supinum
Polygonum viviparum
Erigeron uniflorus

Ranunculus glacialis
Cerastium alpinum
Silene acaulis

Cetraria islandica

These were found, with the exception of *Ranunculus glacialis*, growing in patches of *Rhacomitrium canescens* on the stable areas of scree between the outcrops. *Ranunculus glacialis* was found only in moister places without moss. *Kobresia Bellardi* and *Botrychium lunaria*, which are common on the lower rock outcrops, never extend as high as the hilltops. The reason for the occurrence of this hilltop vegetation, which occurs above several hundred feet of almost barren scree, is clearly the stability of its substratum. The lack of contrast between it and the vegetation of the lower screes, as compared with the Kverkfjöll area, arises from the freedom of the lower screes from inundation by blown sand, which almost obliterates all vegetation in that area.

VEGETATION OF A NUNATAK

In addition to the examination of the different types of vegetation described above, an opportunity was taken of investigating the flora of a nunatak lying about 7 miles from the northern edge of Vatnajökull. The nunatak was a hill about 700 ft. above the general level of the ice, and was about half a mile in breadth. It was composed mainly of loose basalt scree, but on the summit the rock outcropped in several places and offered a more stable surface for colonization. In the steepest parts of the screes no vegetation at all was found, and this is hardly surprising considering the ease with which the rocks were set in motion. On more stable parts, occasional plants of *Cerastium alpinum* and *Saxifraga oppositifolia* occurred. In contrast to this, however, on the static rock at the summit, the moss *Rhacomitrium canescens* formed a thick carpet in which grew the following:

Ranunculus glacialis	a.	Saxifraga oppositifolia	f.
Silene acaulis	f.	S. rivularis	f.
Cerastium alpinum	f.	Poa alpina	o.

In addition to these, in damp hollows there was an abundant growth of *Saxifraga hypnoides*, *S. cernua*, and *S. nivalis*. On stable rock surfaces the lichens *Usnea melanoxantha*, *Gyrophora cylindrica*, *Rhizocarpon geographicum*, *Stereocaulon denudatum*, *Umbilicaria erosa*, were found in fair quantities.

The nearest land surface to this nunatak is 7 miles away, and its vegetation therefore forms a self-contained unit existing under conditions roughly parallel with those of many mountain tops in Britain during the Quaternary Ice Age. The above list goes to show that these plants at least can stand the hardship of growing in a habitat completely surrounded by ice. Moreover, the total area of the nunatak where these plants grew was small enough to reduce considerably the chance arrival of any wind- or animal-borne seed, and to this fact probably can be assigned the absence of certain plants which are normally the associates of those actually found. *Arabis petraea* and *Thymus serpyllum* would be expected where *Ranunculus glacialis*, *Silene acaulis* and *Saxifraga oppositifolia* can grow. Moreover, *S. cernua* and *S. rivularis* are rarely found at great heights in Iceland and strongly suggest that the conditions of life on the nunatak are by no means very severe. Chance dispersal seems to have played a considerable part in this case in determining the species present, and it is tempting to conclude that on a nunatak of larger size a far greater number of species would be found.

TYPES OF PLANT SUCCESSION

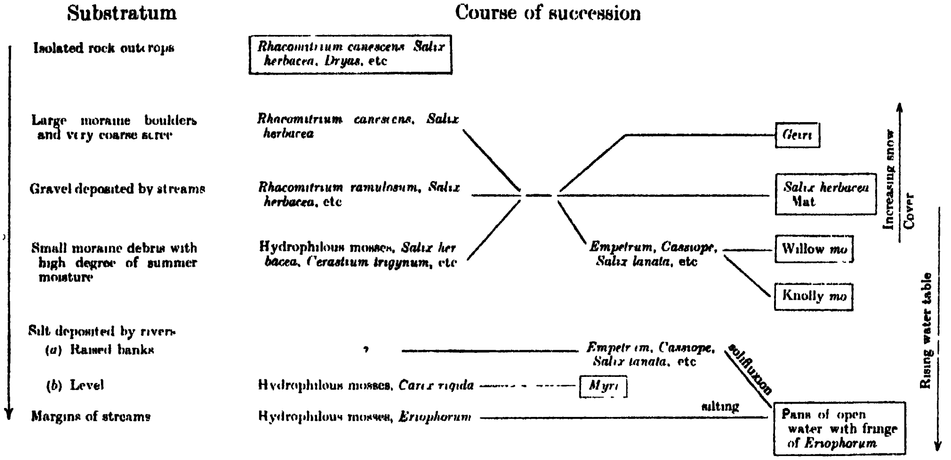
In an area so comparatively recently ice-covered as the land abutting on the northern edge of Vatnajökull, it seems possible that the stages in colonization should be traceable simply by comparing the development of the vegetation at increasing distances from the ice front. This simple method fails for two reasons. In the first place, the advances and retreats of the Icelandic glaciers are extremely complicated, and though in most localities it is clear that a general advance, starting in the Middle Ages and continuing until the end of the last century, is now being followed by a retreat, there is little indication of this in the Snaefell area. In the second place, retreat of the glaciers, where it is evident, does not leave a bare, firm surface of rock, but only a mass of moraine, which includes loose rock of all sizes. On such a substratum plant succession is a precarious process and cannot be deduced with any certainty from observations over a short period. From the preceding account of the various types of vegetation, however, it is clear that colonization takes place on four different kinds of substratum, and the relation of these seres will now be discussed.

The mesosere on the silt deposited by rivers, which leads to the formation of *myri*, and that on the shingle of old stream fans, which leads to the formation of *mo*, have already been described. The abortive lithosere taking place on rock outcrops has likewise been discussed, but no evidence has been brought forward concerning the development of the *mo* on the hillsides. That this cannot have been identical with the mesosere of the shingle fans is certain both from the difference in the substratum and in the greater depth of the water table below soil-level. A certain amount of evidence, however, is available. Before the first stages of colonization the hillside must have been covered with scree or moraine debris of a fairly coarse size (i.e. particles of not less than 3 in. in diameter), just as the land bordering the ice is covered with similar debris at the present time. The initial stage of colonization depends on the degree of weathering of the rocks. Where these do not exceed 6 in. in diameter, their sides are sufficiently moist for a mesosere to proceed. A carpet of hydrophilous mosses is developed with *Salix herbacea*, *Cerastium trigynum* and numerous species of *Saxifraga* growing in it. If, on the other hand, there are larger boulders, colonization is slower, and a lithosere of the type described on p. 21 will proceed. In this case, such a lithosere need not be abortive, for in course of time *Rhacomitrium canescens*, which appears to be the pioneer, fills the cracks between the boulders and a closed community of the moss, and its phanerogamic associates occupies a gradually increasing area, the tops of the boulders only remaining bare or possessing an open association of mosses and *Saxifraga oppositifolia*. From the stages so far described the two seres gradually merge into one. In both a rapid increase in soil takes place by the accumulation of blown sand, which is held by the upgrowing vegetation, thus lowering the available soil moisture in the first case and raising it in the second. Beyond this stage, further progress in colonization was not observed, but it seems highly probable that the course of the succession would thenceforward follow that which occurs on the shingle of the stream fans with invasion of the larger *Salix* spp. and other shrubs and the rapid accumulation of wind-deposited soil.

The interrelationships of the various types of succession can now be summarized and the result is shown diagrammatically in Table 2. Seven apparent vegetational climaxes are shown, the most important of which are the willow *mo* and the *myri* and *floi*. There can be no doubt that these are true climaxes within normal time limits, providing that the climate remains unchanged. With a very slight amelioration of climate, however, *Betula nana* would undoubtedly invade the willow *mo* and the drier parts of the *myri*, though a considerably larger rise in the summer temperature would be needed for the growth of *Betula pubescens*. It is difficult to tell how far such a rise in temperature would affect the *myri*. By thawing the soil in the summer a great obstacle to the growth of deeply rooted plants would be removed, but it must be remembered that similar *myri* covers a large part of the lowlands of Iceland, even in sheltered positions, and *myri* is thus considered a climatic climax. This, however, is by no means certain, since such areas of *myri* are always extensively grazed, and the biotic factor alone may be responsible for its existence. Only experiments with enclosures could decide the point.

Table 2. *Types of plant succession on different substrata*

The effects of snow cover and the height of soil above the water table are summarized on the right of the table. Apparent climax communities are shown enclosed in panels.


Substratum
Course of succession
Isolated rock outcrops
Rhacomitrium canescens Salix herbacea, Dryas, etc
Large moraine boulders and very coarse scree
Rhacomitrium canescens, Salix herbacea
Gravel deposited by streams
Rhacomitrium ramulosum, Salix herbacea, etc
Small moraine debris with high degree of summer moisture
Hydrophilous mosses, Salix herbacea, Cerastium trigynum, etc
Silt deposited by rivers
(a) Raised banks
?
(b) Level
Hydrophilous mosses, Carex rigida
Margins of streams
Hydrophilous mosses, Eriophorum
Geiri
Salix herbacea Mat
Empetrum, Cassiope, Salix lanata, etc
Willow mo
Knolly mo
Empetrum, Cassiope, Salix lanata, etc
Myri
solifluxion
silting
Pans of open water with fringe of Eriophorum
Increasing snow Cover
Rising water table

Animal communities

In the limited time available it was not possible to attempt a thorough survey of the animal life of the area, and instead it was thought best to study the relationships of the most abundant species. The results of this brief survey are presented under three headings:

(*a*) Aquatic invertebrates (no aquatic vertebrates were recorded),
(*b*) Terrestrial invertebrates,
(*c*) Terrestrial vertebrates,

and the relationships of the community in sections (*b*) and (*c*) are then discussed.

(*a*) *Aquatic invertebrates*

In the special area, the only habitats available for aquatic animal life were the pools in the marsh and the streams draining the hillside. These both proved singularly sterile, the former harbouring a single species of snail, *Limnaea pereger*, and an occasional *Agabus bipustulatus*, and the latter in many places being rich in the larvae of caddis flies and of *Simulium vittatum*. Beyond the limits of the special area, however, aquatic invertebrates were found in considerable numbers in two localities. The pools in the marshes on the west of Snaefell, which resembled those on the east, though they were deeper (in some places reaching 2½ ft. (0·8 m.)) and probably older in origin, contained a rich fauna, which was not collected, but, as far as inspection by eye could tell, was identical with that of the second locality. This second locality is very surprising, viz. the pools on the terminal moraine of Eyjabakkajökull. Most of the pools did not exceed 6 ft. (2 m.) in breadth and 2 ft. (0·6 m.) in depth. They had a moderate growth of filamentous, green algae at the bottom and they were mostly on the older part of the moraine, though some were on new moraine and even in contact with ice. In such circumstances it was surprising to find any animal life in them at all, but in spite of the unpromising conditions they contained a plankton only slightly less dense than that of an English pond at its summer maximum. This plankton consisted of the following Cladocera, Copepods and Ostracods:

Daphnia pulex
Diaptomus gracilioides
Cyclops strenuus
Eucypris glacialis
E. affinis hirsutus

Together with these there were numerous individuals of the beetle, *Agabus bipustulatus*, and the phyllopod, *Lepidurus glacialis*, the former swimming in its usual manner through the water, the latter burrowing through the debris at the bottom of the pools.

This fauna, small though it is, appears to be of considerable interest from the point of view of the survival of animal life in glaciated regions. Without doubt these pools are frozen solid in winter and similar pools, offering an equally long unfrozen period in the summer, would exist on a *nunatak* of any size. Hence it seems fair to conclude that a similar fauna might well exist through a glacial epoch on the moraines bordering a *nunatak*, even of small size, and this conclusion is perhaps of some importance since animal geographers, relying on the remarkable powers of distribution of the Crustacea (presumably in the nauplius stage) and of the water beetles, would be inclined to regard such a fauna as a post-glacial introduction.

The community is of some interest, also, from the ecological point of view, since it appears to consist entirely of plant and detritus feeders. No macroscopic carnivore appeared to be present, and it is hard to see where such a carnivore could come from, since the only birds which occur near the terminal moraines are whooper swans, which are always herbivorous. It is surprising that the char is absent from these pools, since in Iceland it is a surface fish, by no means uncommon in shallow, stagnant pools.

(*b*) *Terrestrial invertebrates*

The invertebrate life of the special area was investigated in a superficial manner only by collecting from the usual habitats, e.g. around the roots of plants, under stones and in moss. An attempt to put the investigations on a quantitative basis is described below. Since the marsh proved almost sterile, attention was concentrated mainly on the willow *mo* and the stream banks. By so doing, a number of beetles (mainly Brachelytra), chironomids and possibly spiders was overlooked, but the investigation of the marsh would only have been profitable if much time could have been afforded with a Berlese funnel.

On p. 6 the digging of pits to investigate soil profiles is described. These pits had vertical walls (see Pl. 1, phot. 2), and since they were dug to below the depth of the water table, they made excellent insect traps. After it was discovered that insects which had fallen into the traps could not escape, it was decided to visit four of the pits every morning and collect all the animal life which had fallen into them for identification and analysis. The pits clearly offered only an approximate method for a quantitative investigation of the animal life, since they were certain to be selective in operation, and their limitations must be considered before an estimate of their value can be made. The disadvantages of the pits seem to be the following:

(i) No reliability can be placed on records of aerial insects since their occurrence can only be a matter of chance.

(ii) It is hard to tell how far an insect or other small invertebrate falling into a pit is fortuitous. Experience, intelligence, or slow deliberate movements may result in a relatively abundant species appearing as less numerous than in fact it is. If one watches a beetle or a harvestman moving, however, it is hard to believe that any of the factors mentioned above are significant, and the results obtained from the pit analyses agree with the impression obtained from general collecting.

(iii) There is a danger in as great a period as 24 hr. that an animal falling into the pit will be lost. This again, however, seems to be small, since the water in the pits was very shallow (never more than 3 in.), and there was no difficulty in seeing the bottom. It is interesting to note in this connexion that the insects were always found alive and floating, whereas spiders and harvestmen apparently drowned quickly and sank to the bottom, hence there is a greater chance that they may have been underestimated.

The advantages of the pit method of obtaining a rough, quantitative survey are that it gives very quick results, and if continued over a long period it seems likely that it would give information not only about relative numbers, but also about the movement of insects in varying weather conditions and at different times of day. With this last purpose in mind, it was originally intended to collect the contents of the pits twice every 24 hr., but lack of time prevented this. It was clear, however, that the morning and evening collections differed markedly. The two species of *Otiorrhynchus*, for example, were only taken at the morning collection (8 a.m.), and were therefore nocturnal in their movements, which agrees with the observation of Lindroth (1931, p. 232), while *Mitopus morio* was taken chiefly, but not exclusively, in the evening collection and is therefore mainly diurnal. The effects of high winds are also evident from the analysis of the results, but it is possible to interpret the falling off in numbers that occurs on 19 August as evidence of increased experience of the invertebrate population or even of a decreasing population resulting from the number of animals already trapped, though this seems unlikely. Only trials extending over a longer period would establish the efficiency of this method in animal ecology.

The results of the pit method of collecting are given in Table 3 and need little explanation. By comparison with Table 1 it will be seen that the pits differ in the extent of the vegetation covering round them as well as in the soil moisture as judged by the depth of the water table, and it is not possible to separate these two factors completely in analysing the result. Pit no. 5 differs from the others in its low but close covering of vegetation, which did not exceed 2 in. (5 cm.) in height; its water table stands at an intermediate height. Pit no. 3 differs from the rest in that its soil is notably moister than that of the others; it resembles pits nos. 2 and 8 in the taller vegetation, but the covering round it is considerably closer. Pits nos. 2 and 8 have a comparatively open vegetation, where solifluction has been recently active. All the pits had approximately equal perimeters with the exception of no. 8, for which the results should be halved to make them comparable with the others. The conclusions from the table mainly concern three species:

(1) *Mitopus morio.* This is the most abundant species in each locality. The table suggests that its particular abundance in pit no. 3 is associated with the greater soil moisture rather than with the close cover, since it is still numerous at no. 1 with its low vegetation covering.

(2) *Otiorrhynchus* spp. As Lindroth has observed, the two species of *Otiorrhynchus* spend the day under stones and emerge only by night. This was confirmed by observations at ,Snaefell, the beetles being taken with fair regularity under stones on the stream banks. The table suggests that the increased soil moisture is a favourable factor for the beetle, presumably operating indirectly in that it increases the number of suitable day resting places.

(3) *Amara quenseli.* The figures for this species are most striking and seem clearly to show that the beetle is most abundant in low cover. Lindroth refers to it as occurring in dry, sandy places, and for this reason perhaps it is absent from pit no. 3, but cover must play a large part, since it is absent also from pits nos. 2 and 4.

In the case of the other species mentioned in Table 2, the figures are not conclusive and serve only to show the lack of any particular habitat preference. One further point, however, is of importance, which will be referred to later. In the analyses of the crop contents of birds, the relative abundance of the invertebrate species was found to be almost identical with that of the pits, with the exception that the birds had taken in addition such flying insects as caddis flies. This seems to indicate clearly the non-selective feeding of birds, which has been commented on before for Iceland by Roberts (1934) among other writers.

Table 3. *Data obtained on distribution of invertebrates*

No. of pit	Date	Weather				Arachnida		Coleoptera					Diptera									Lepidoptera		
		Temperature at 9 a.m.	Temperature at 9 p.m.	Wind (capitals denote high velocity)	Rain (for symbols, see below)	*Lycosa tarsalis*	*Milopus morio*	*Otiorrhynchusdubius*	*Otiorrhynchus arcticus*	*Aphodius lapponum*	*Amara quenseli*	*Byrrhus fasciatus*	*Scatophaga stercoraria*	*Scatophaga furcatum*	*Chironomus* sp.	*Exechia frigida*	*Helophilus pendulus*	*Phoridae* sp.	*Agromyzidae*	*Graphomyia maculata*	*Anthomyidae*	*Crymodes exilis*	Total
5	13. viii	54°	43°	n.	R.	.	6	.	.	1	5	1	2	.	.	.	.	.	.	.	1	.	16
	14. viii	52°	40°	s.w.	—	.	6	.	.	.	2	.	.	1	.	.	.	.	.	1	.	.	10
	15. viii	51°	41°	e.	m.r.	1	.	.	.	1	1	.	.	.	1	.	.	.	.	.	.	.	4
	16. viii	54°	40°	s.e.	sh.	.	2	.	.	.	1	.	.	.	1	.	1	.	.	.	.	.	5
	17. viii	51°	40·5°	s.e.	—	.	1	.	.	.	2	.	.	.	1	.	.	.	.	.	.	.	4
	18. viii	50·5°	40·5°	s.e.	r., f.	.	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	5
	19. viii	53°	39·5°	S.E.	e.r.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
					Totals	1	17	.	.	3	13	1	2	1	3	.	1	.	.	1	1	1	45
3	13. viii	54°	43°	n.	R.	1	8	2	.	.	.	1	.	.	1	.	.	.	.	.	.	.	13
	14. viii	52°	40°	s.w.	—	.	12	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	13
	15. viii	51°	41°	e.	m.r.	1	1	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	4
	16. viii	54°	40°	s.e.	sh.	.	.	1	.	.	.	1	.	.	1	1	.	1	.	.	.	.	5
	17. viii	51°	40·5°	s.e.	—	.	6	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	7
	18. viii	50·5°	40·5°	s.e.	r., f.	.	6	1	.	.	.	.	.	.	1	.	.	1	.	.	.	.	9
	19. viii	53°	39·5°	S.E.	e.r.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	3
					Totals	2	34	5	1	.	1	2	.	.	4	1	.	3	.	1	.	.	54
8	13. viii	54°	43°	n.	R.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	14. viii	52°	40°	s.w.	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	15. viii	51°	41°	e.	m.r.	1	.	.	.	.	.		.	.	.	.	.	.	1	.	.	.	2
	16. viii	54°	40°	s.e.	sh.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	17. viii	51°	40·5°	s.e.	—	.	5	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	8
	18. viii	50·5°	40·5°	s.e.	r., f.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	19. viii	53°	39·5°	S.E.	e.r.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
					Totals	1	6	.	.	.	1	.	.	.	2	.	.	.	1	.	.	.	11
2	13. viii	54°	43°	n.	R.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	14. viii	52°	40°	s.w.	—	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
	15. viii	51°	41°	e.	m.r.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	2
	16. viii	54°	40°	s.e.	sh.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	17. viii	51°	40·5°	s.e.	—	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2
	18. viii	50·5°	40·5°	s.e.	r., f.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
	19. viii	53°	39·5°	S.E.	e.r.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
					Totals	.	14	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	17
					Totals	4	71	5	1	4	15	4	3	1	9	1	1	3	1	2	1	1	127

Symbols for rain: R. = heavy rain; m.r. = morning rain; sh. = showers; r. = light rain; f. = fog, e.r. = evening rain.

Apart from the three most abundant invertebrates, whose distribution and habits are given above, the invertebrate fauna is mostly easily considered in two divisions: the terrestrial forms and volant forms. In addition to the beetles and Arachnida mentioned in Table 3, the following also occurred less abundantly: the spider, *Arctosa alpigena*, the beetles, *Patrobus sententrionis* and *Atheta atramentaria*, and numerous Collembola. These were found throughout the willow *mo*. By the banks of streams, the snail, *Oxychilus alliarius*, was found usually under stones, together with a small, unidentified species of earthworm. This community, with the exception of the spiders and harvestmen, feeds entirely on plants and refuse. In its turn it forms the food of the birds (see p. 33).

In bright, sunny weather, there is abundant animal life above the willow community. In addition to the species in Table 3 the moths *Cidaria caesiata*, *Laodamia fusca*, *Pyrausta torvalis*, the gall-flies *Plectrocus* sp., *Barycnemis* sp., *Hemiteles* sp. and a species of chalcid are present in moderate numbers, together with a fly of the family Agromyziidae. More abundant than these are the Trichoptera: *Limnophilus picturatus*, *L. griseus*, *L. sparsus* and *Apatania arctica*. In August 1937 the first of these was swarming and was to be found in very great numbers from the river bank even to the summit of Snaefell (easily an altitude record for any Icelandic insect!).

Round sheep dung the usual creophilous community occurred, the flies consisting of *Scatophaga stercoraria*, *S. furcatum*, *Calliphora erythrocephala* and *Cynomyia mortuorum*. The beetle, *Aphodius lapponum*, and various small Brachelytra occurred in and under the dung.

(c) *Terrestrial vertebrates*

By far the most numerous and important members of the vertebrate fauna of the Snaefell area are the birds. These have already been fully described by Wilson (1937) and need only be mentioned here in as far as they affect the rest of the animal and plant life. In addition to them, three species of mammals are present, but no fishes were recorded, though char are probably present in the river. The three mammal species are the sheep, the arctic fox and the reindeer. As already mentioned, sheep are almost confined to the moraine of Eyjabakkajökull, and their effect on the vegetation by feeding is small. Their presence, however, is responsible for the main part of the creophilous community, and if they were excluded from the area such insects as *Aphodius lapponum* and *Cynomyia mortuorum* would doubtless disappear. The arctic fox is probably a rare animal in the district. About 5 miles north of the camp, one earth was seen, at the mouth of which were numerous bones of birds, probably golden plover. From an ecological point of view, the fox stands at the apex of the animal pyramid of numbers, but because of its scarcity it can only play a small part in controlling the bird life. Even in the highlands it is frequently destroyed by man, and this is certainly the chief cause of its scarcity. It is possible, too, that the country is too open for it, for it is said still to be common in the post-glacial lava flows of the western highlands.

Reindeer were never seen, but they are well known to be present. They are not indigenous to Iceland, but are descendants of animals introduced in 1771. The herds at present number several hundreds. Though they have been shot in the neighbourhood of Snaefell, they probably spend more of their time further east where their food is more abundant. The amount of lichens, and particularly of *Cladonia rangiferina*, increases rapidly on going eastwards from Snaefell, lichen communities covering large areas on the mountains east of the Jökulsá i Fljotsdal, and it is probably this factor which restricts the distribution of reindeer to the eastern highlands.

A complete list of the seventeen species of birds observed is included at the end of this paper. It is a surprisingly large number for the highlands in August, since in 1936 and 1937 observations only started after the migration had begun, and the total number of species must be almost double this. Details of stomach-content analyses are given by Wilson (1937) and these divide the birds into four well-marked groups: herbivores, ground-feeding insectivores, aerial-feeding insectivores, and other carnivores. The first group contains such birds as the whooper swan and the ptarmigan, the former found on the lake at the snout of Eyjabakkajökull, and the latter found chiefly in rocky places at the limit of vegetation. The two groups of insectivores are well defined, the golden plover being typical of the ground-feeding class, while the meadow pipit and the white wagtail are typical aerial feeders. The golden plover crops contained large numbers of *Mitopus morio* with a few beetles or spiders, and occasionally a leaf of willow or a piece of moss, which must have been taken unintentionally in catching the insect. The food was clearly not selected, but consisted only of the most abundant crawling animals present *on the ground*. The meadow pipits and white wagtails showed a similar lack of preference with insects *in the air*. Their food consisted chiefly of caddis flies, which were the most abundant flying insects, with an occasional dung fly or Chironomid. In spite of this lack of selection, neither group trespassed on the food of the other; *Mitopus morio* was never found in the crop of a white wagtail, nor were golden plover found to take caddis flies. The fourth group of birds consists of the birds of prey; the merlin, raven, Arctic skua and the rare Iceland falcon. Of these only the Arctic skua was seen feeding, when a pair killed and ate a wagtail, but the merlins undoubtedly took pipits and the ravens and falcons probably larger prey. The presence of the skua is in itself remarkable so far inland, but the alteration in its habits is perhaps more remarkable since a colony of about a hundred birds was present on the islands in the Jökulsá i Fljotsdal and these presumably had abandoned their normal parasitic life and were preying on the smaller birds in the district.

COMPARISON WITH SURROUNDING DISTRICT

In the preceding sections an attempt has been made to give a brief survey of the plant and animal life of the Snaefell district. In order to show how far this account is true of the semi-glaciated areas of Iceland as a whole, a comparison with the surrounding highlands is necessary. For this purpose analysis of the plant population by Raunkiaer's method is instructive, though in some respects misleading; this follows below together with values given by Hansen for the whole island at varying altitudes[1] (1930, p. 17):

	N	*Pt*	*n*	*Ph*	*Ch*	*H*	*G*	*HH*	*Th*
The whole of Iceland	375	7·4	349	1·1	15·2	52·4	10·6	9·2	11·5
500–600 m. only	117	4·5	112	0	25·0	56·3	8·9	5·4	4·5
600–700 m. only	91	2·2	89	0	29·2	53·9	11·2	3·4	2·2
700–800 m. only	65	3·2	63	0	36·5	46·0	12·7	1·6	3·2
Snaefell district	83	3·8	79	0	30·4	46·8	8·8	5·1	5·1
Kverkfjöll district (Anderson & Falk, 1935)	49	2	48	0	37	43	10	6	2

The most important figures in the above table are those for the chamaephyte percentages, as Hansen has shown that these rise steadily with increasing altitude and give reliable data when compared with those of other arctic and subarctic lands. The figures for the Snaefell district suggest two conclusions: (*a*) that its vegetation is typical of Iceland at an altitude of about 700 m., and (*b*) that the number of species occurring is about normal for its altitude. Neither of these conclusions, though justified by Hansen's figures, is entirely true. Hansen's figures are constructed from lists of plants recorded from various highland localities by such travellers as Herra Pálmi Hannessen and Thoroddsen; they are based, therefore, on the oases in the central desert and not on the desert itself. Consequently, the vegetation of the Snaefell district is typical only when compared with other similar highland oases; it is typical of the most luxuriant vegetation at its own altitude, but not of the vegetation of the highlands as a whole. Much of central Iceland suffers so severely from wind erosion that it is either bare or covered only with *Elymus* dunes; other large areas support an impoverished grassland community, which at present is rapidly diminishing as the result of wind erosion, probably after overgrazing. It is only in a very few places that a vegetation as luxuriant as that of the willow *mo* at Snaefell is to be found. Most, if not all, of these places are in the neighbourhood of the large glaciers and are often protected by glacial rivers from excessive grazing by sheep (e.g. the land north of Hvítárvatn on the east of Langjökull). Protection from sheep, however, is not enough to ensure the development of vegetation, for many areas well guarded from sheep

[1] *N* = total number of vascular plants; *Pt* = percentage of pteridophytes; *n* = number of phanerogams; *Ph* = percentage of phanerophytes; *Ch* = percentage of chamaephytes; *H* = percentage of hemicryptophytes; *G* = percentage of geophytes; *HH* = percentage of helo- and hydrophytes; and *Th* = percentage of therophytes.

are devoid of any closed plant communities. Such areas are sterile because the rock weathers down to a coarse sand, which will not retain enough moisture for the initial colonization by plants. The reason for the comparative luxuriance of the Snaefell vegetation is that the underlying rock has weathered to a finer sand, which retains moisture sufficiently to allow the development of the initial stage of colonization and to prevent the frequent occurrence of sand storms. How far this difference in the size of the rock particles is simply due to age and how far to differences in structure, it is impossible to say.

A further reason for the extreme difference in the abundance of both plant and animal life between the Snaefell district and such a highland oasis as Hvannalindir (Anderson & Falk, 1935) is the cumulative nature of plant and animal colonization. The greatest obstacle to plant colonization in the Icelandic highlands is the maintenance of a closed community. Once an open community with *Salix herbacea* as a dominant has developed, further colonization up to the willow *mo* stage appears to proceed rapidly, but at this stage retrogression through wind erosion, solifluction or the undercutting of streams seems almost invariably to occur and may proceed with such violence that the whole area is denuded. Where this does not occur, colonization, by animals especially, can proceed with great rapidity. The *S. herbacea* stage of colonization having one canopy only, cannot include a large number of plant species, nor, through its lack of cover, can it shelter more than a very small insect fauna. Willow *mo*, on the other hand, is a three-layered community, and the number of plant species in it is more than proportionately greater than in *S. herbacea* mat. Similarly, the greater cover causes an increase in such animals as the *Geodephaga*, *Otiorrhynchus* spp. and *Mitopus morio*, which is reflected in the abundance of the golden plover and the consequent presence of birds of prey.

CONCLUSIONS

If comparison is now made between the vegetation of Snaefell and the sub-arctic vegetation of the mountain tops in the British Isles, two important factors hindering the development of Icelandic vegetation become apparent. In the first place, the Snaefell rock is a worse substratum for plant colonization than most British rock. It weathers too rapidly in the unfavourable climatic conditions at high altitudes for such a lithosere to take place as is found in the English lake district or as that described by Polunin (1936) for Norwegian Lapland. In addition, even at Snaefell, the scree formed by weathering of the rocks is less stable than most British scree. In the second place, though the flora of Iceland bears a close relationship with that of Britain, its isolated position has resulted in an impoverishment, which cannot be accounted for by climate alone. The extent to which this impoverishment of the flora restricts the quality of the vegetation when compared with British subarctic standards can be estimated approximately from the figures of Matthews (1937). If the northern and Arctic components of the British flora only are considered, the following figures are obtained:

	Great Britain	Iceland as a whole	Snaefell only
Northern continental	91	37	4
Northern montane	25	12	2
Arctic-subarctic	30	17	6
Arctic-alpine	76	60	38
	222	126	50

Of these four elements, therefore, Iceland as a whole has 57% of the British total; while of those that occur in Iceland only 40% are found at Snaefell.

If for the purposes of calculation it is assumed:

(*a*) That the occurrence of these species in any particular part of Iceland is purely accidental;

(*b*) That the mechanism of their dispersal to Iceland had been entirely non-selective;

(*c*) That the agency of selection would act no more stringently on those species that are absent from Iceland than on those now present there (i.e. 40% being able to tolerate the Snaefell conditions);

Then it follows that if all the 222 species occurring in Great Britain could have been dispersed to Iceland, the addition to the Snaefell flora would be 40% of 222–126 or 38.

Since in fact dispersal to Iceland must have been partly selective and since it is unlikely that those species absent from Iceland would be as well suited for the Snaefell conditions as those present in Iceland, this figure is certainly an overestimate. We may conclude, therefore, that the impoverishment in the Icelandic flora for geographical reasons cannot be responsible for the absence of more than some thirty species when compared with Great Britain. Furthermore, if instead of comparing numbers the life forms of the plants are compared, it is still found that no great difference in the form of the vegetation is likely to occur.

With the two limitations outlined above in mind, it may be claimed therefore that the Snaefell animal and plant populations present some resemblance to those of the semi-glaciated areas of Britain at the close of the Quaternary Ice Age.

SUMMARY OF SPECIES MENTIONED

The following list of species is given for purposes of reference. It includes all the species of animals and plants collected, most of which have already been mentioned. As regards the comprehensiveness of the list, it should be noted that only the list of flowering plants can be claimed to approach completeness. The collections were made during two visits, both in August, and at that time of year the omissions from the collection of flowering plants were probably small. On the other hand, the number of other plants must be much greater than that shown, since far more time was needed for collecting them than was available. The list of animals is even less complete than that of the plants. The birds were studied with the same thoroughness as the flowering plants, but migration had started before their study could begin, and such absentees as the red-necked phalarope and all the duck must be accounted for by this. The list of insects is particularly incomplete, partly because of the seasonal variations in the insect population, and partly through lack of opportunity for collecting. Nevertheless, though the lists give no reliable information of the relative or absolute numbers of species, from the close similarity of the collections made in the two visits to Snaefell, it appears that the most abundant species are likely to be mentioned.

(Where only orders or classes and not species have been determined, the number of species present has been taken as one; the totals given are therefore always the minimum.)

ANIMALS (65 spp.)

Mammalia (2 spp.):

Alopex lagopus (Arctic fox)
Rangifer tarandus (reindeer)

Aves[1] (17 spp.):

Cygnus c. islandicus Brehm (Iceland whooper swan)
Phalaropus fulicarius jourdaini Iredale (grey phalarope)
Motacilla alba alba L. (white wagtail)
Anthus pratensis L. (meadow pipit)
Lagopus mutus islandorum Faber (Iceland ptarmigan)
Capella gallinago faroeensis C. L. Brehm (Faroe snipe)
Goose spp. (probably grey lag and pink foot)
Falco columbarius subaesalon Brehm (merlin)
Falco rusticolus islandus Brunn (Iceland falcon)
Oenanthe o. leucorrhoa Gm. (wheatear)
Plectrophenax nivalis insulae Salomonsen (snow bunting)
Corvus corax tibetanus Hodgson (Iceland raven)
Charadrius apricarius apricarius L. (golden plover)
Calidris alpina alpina L. (dunlin)
Erolia maritima maritima Brunn (purple sandpiper)
Stercorarius parasiticus L. (arctic skua)

Insecta[2] (34 spp.):

COLLEMBOLA (1 sp.):
Species not ascertained

TRICHOPTERA (4 spp.):
Limnophilus picturatus McLachl.
L. griseus L.
L. sparsus Curt.
Apatellia zonella Zett.
(= Apatania arctica Boh.)

COLEOPTERA (8 spp.):
Carabidae:
Patrobus septentrionis Dej.
Amara Quenseli Schonh.
Dytiscidae:
Agabus Solieri Aubé
Staphylinidae:
Atheta atramentaria Gyll.
Scarabaeidae:
Aphodius lapponum Gyll.
Byrrhidae:
Byrrhus fasciatus Forst.
Circulionidae:
Otiorrhynchus arcticus O. Fabr.
O. dubius Strom.

LEPIDOPTERA (4 spp.):
Noctuidae:
Crymodes exulis Lef.
Geometridae:
Cidaria caesiata Schiff.
Pyralidae:
Salebria fusca Haw.
Pyrausta torvalis

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[1] Nomenclature of Hachisuka, M. U. (1927).

[2] Nomenclature of Lindroth, C. H. (1931).

DIPTERA (13 spp.):

Tipulidae:
Tipula rufina Meig.
Simuliidae:
Simulium vittatum Zett.
Chironomidae:
Chironomus, sp.
Fungivoridae:
Exechia frigida
Syrphidae:
Heliophilus pendulus L.
Phoridae:
Species not ascertained
Cordyluridae:
Scopeuma (=Scatophaga) stercoraria L.
S. squalidum Meig.
Anthomyidae:
Species not ascertained
Agromyzidae:
Species not ascertained
Tachinidae:
Calliphora erythrocephala Meig.
Cynomyia mortuorum L.
Muscidae:
Graphomyia maculata Scop.

HYMENOPTERA (4 spp.):

Plectrocus sp.
Barycnemis sp.
Hemiteles sp.
Chalcid sp.

Arachnida (3 spp.):

Araneida:
Lycosa tarsalis Sh.
Arctosa alpigena Dol.
Phalangidea:
Mitopus morio Fabr.

Crustacea (6 spp.):

Phyllopoda:
Lepidurus glacialis Kr.
Copepoda:
Diaptomus graciloides Lilljeborg
Cyclops strenuus Fischer
Cladocera:
Daphnia pulex de G.
Ostracoda:
Eucypris glacialis Sars.
E. affinis hirsutus Fischer

Mollusca (2 spp.):

Limnaea pereger Müller
Oxychilus alliarius Miller[1]

Annelida (1 sp.):

1 species of the Lumbricidae, species not ascertained

PLANTS (114 spp.)

Angiosperms[2] (80 spp.):

*Alchemilla glomerulans
*A. minor
Alsine rubella
Arabis alpina
A. petraea
Armeria maritima
Bartsia alpina
Betula nana
Calamagrostis neglecta
Cardamine pratensis
Carex Goodenoughii
C. Lyngbyei
C. rariflora
C. rigida
C. rostrata
Cassiope tetragona
Cerastium alpinum
C. triviale
Deschampsia alpina
Draba alpina
Dryas octopetala
Empetrum hermaphroditum
Epilobium alsinefolium
E. latifolium
Erigeron uniflorus
Eriophorum polystachion
Eriophorum Scheuchzeri
*Euphrasia frigida
Galium sylvestre
Gentiana campestris
G. nivalis
G. tenella
Geranium sylvestris
Gnaphalium supinum
*Hieracium petiolosum
Juncus arcticus
J. trifidius
*Kobresia Bellardi
Loisleuria procumbens
Luzula spicata
Oxyria digyna
Pedicularis flammea
Phleum alpinum
Poa alpina var. vivipara
Potentilla alpestris
P. palustris
Polygonum viviparum
Pyrola minor
Ranunculus acris
R. glacialis
R. pygmaeus
Rumex acetosa

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[1] Identification somewhat doubtful: the specimen unfortunately has not been preserved.
[2] Nomenclature of Ostenfeld & Gröntved (1934).

Angiosperms[1] *continued*:

Sagina procumbens
S. Linnaei
Salix glauca
S. herbacea
S. lanata
S. phylicifolia
Saxifraga cernua
S. groenlandica
S. hirculus
S. nivalis
S. oppositifolia
S. rivularis
S. stellaris
S. hypnoides
Sedum roseum
S. villosum
Sibbaldia procumbens
Silene acaulis
S. maritima
*Taraxacum devians
Thalictrum alpinum
Thymus serpyllum
Tofieldia palustris
Vaccinium uliginosum
Veronica alpina
V. fruticans
Viscaria alpina
Zannichellia palustris

Pteridophyta (3 spp.):

Botrychium lunaria
Selaginella selaginoides
Equisetum arvense

Bryophyta (31 spp.):

Musci (21 spp.):

Amblystegium riparium (Hedw.) B. & S.
Aulacomnium palustre (Schwaeg.)
Bartramia ithyphylla Brid.
Calliergon (Hypnum) stramineum (Dicks) Kindb.
Climacium dendroides W. & M.
Camptothecium nitens (Hedw.) Schp.
Cynodontium virens (Hedw.) Schp. var. Wahlenbergii Schp.
Desmatodon latifolius (Hedw.) B. & S. var. muticus Brid.
Dichodontium pellucidum (Hedw.) Schp.
Drepanocladus (Hypnum) exannulatus (Gumb.) Moenk.
D. (Hypnum) uncinnatus (Lind.) W.
Mniobryum albicans (Wahl.) Limpr. var. glaciale (Schleich) Limpr.
Mnium affine Bland. var. elatum B. & S.
Paludella squarrosa Brid.
Philonotis tomentella Mol.
Polytrichum juniperinum (Hedw.)
P. ramulosum Lindb.
Rhacomitrium canescens Brid.
Sphagnum teres Angst. var. imbricatum W.
Splachnum vasculosum Hedw.
Webera cruda (Hews.) Schwaeg.

Hepaticae (2 spp.):

Marchantia polymorpha, L.
Preissia quadrata Nees.

Lichens (8 spp.):

Usnea melanoxantha Ach. and G.
Peltigera aphthosa Willd.
Rhizocarpon geographicum (L.) D.C.
Umbilicaria crosa (Web.) Ach. Gyrophora crosa of the B.M. Handbook)
Cetraria islandica
Gyrophora cylindrica Ach.
Stereocaulon denudatum Flk.
Alectoria (Subparmelia) pubescens (L.) Howe jr. (Parmelia pubescens of the B.M. Handbook)

The work of identification of the plants and animals in the above list was divided as follows:

Flowering plants marked with asterisk (*): A. J. Wilmott, British Museum.

Mosses: P. W. Richards, Cambridge.

Lichens and Liverworts: E. W. Jones, School of Forestry, Oxford; I. M. Lamb, British Museum.

Coleoptera and Lepidoptera: K. G. Blair, British Museum.

Trichoptera: M. E. Mosely, British Museum.

Hymenoptera: J. F. Perkins, British Museum.

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[1] Nomenclature of Ostenfeld and Gröntved (1934).

Diptera: R. L. Coe and F. W. Edwards, British Museum.
Arachnida: A. R. Jackson, Chester.
Crustacea: I. Gordon, British Museum.
Mollusca: J. C. Vickery, British Museum.

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SUMMARY

1. The climatic, physiographic and edaphic conditions of the Snaefell area of the highlands of Iceland are described.

2. An account follows of the principal plant communities, viz. *myri*, colonized stream fans, willow *mo*, knolly *mo*, *geiri*, stream banks and such open types of community as those of rock outcrops, screes and hilltops.

3. The types of succession leading up to these communities are described, with particular emphasis on such geomorphological topics as the origin of pans in *myri* and the effects of erosion by wind, solifluction and snow.

4. The interrelationships between the different lines of succession are considered.

5. The most conspicuous components of the animal population are described and an account is given of an attempt to give the survey of the ground fauna a numerical basis.

6. The animal and plant populations of the Snaefell area are compared (*a*) with those of the surrounding highlands (as typifying a semi-glaciated district) and (*b*) with those of the highlands of Great Britain. From these comparisons an attempt is made to discover how far the fauna and flora of the Snaefell area help in constructing a picture of post-glacial Britain.

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STUDIES IN THE ECOLOGY OF BRECKLAND

IV. THE GRASS-HEATH

By A. S. WATT

(*With Plates* 3–5 *and six Figures in the Text*)

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INTRODUCTION

IN an earlier paper (Watt, 1936) it was stated that soil is an important factor differentiating the vegetation of Breckland. This statement is now substantiated for what is commonly called the "grass-heath". Seven soil types, corresponding to seven stages in the development of a podsol, bear different types of grass-heath. These are provisionally called grasslands A, B, C, D, E, F and G, and for convenience these letters are used for the corresponding soil types, A having the youngest and G the most mature profile.

It may be well to state now that no suggestion is made or implied that all the different stages of soil-profile development have necessarily proceeded directly from one to the next in the series under the cover of the respective grasslands. Nothing so simple is likely, perhaps even possible. All that is done here is to demonstrate the importance of the soil as a causal factor of variation. At the same time the opportunity is taken of characterizing the different grasslands studied.

The material described is from Lakenheath Warren where all the four major physiognomic communities of Breckland vegetation—heather, bracken, sand-sedge, grass-heath—are found. Of these the grass-heath was selected for primary attention, and areas free or almost free from heather, bracken and sand-sedge were chosen for analysis. But it ought to be made clear that sand-sedge and bracken can and do grow in all soil types from A to G, heather from B to G.

All the grassland types are grazed by rabbits.

The different grassland communities cover areas of widely different size: A, in small to large patches from a few square metres to about 1500 sq. m.—all within an area of about ½ sq. mile: B covers the largest area, in patches up to 200–300 acres: the rest smaller areas of 5–10 acres each. Within each type a minimum of fourteen plots was selected more or less at random, but as far as possible avoiding rabbit burrows. In practice complete exclusion was impossible with plots of the size used. The size and form of the plots in C to G was 5 × 30 m.: in B, 20 × 20 m., and in A the unit was the patch itself usually about 25–40 sq. m. where it was small, and where larger it was split up into areas of a size similar to the smaller patches. All the plots were marked and numbered. In the analysis of the vegetation the ordinary "British" symbols of frequency were used. Data for the higher plants were recorded during the spring and summer months and expressed numerically to obtain figures for average abundance in the way and with the reservations already stated (Watt, 1934). The data for bryophytes and lichens were obtained during the winter and early spring months. The collection of data was spread over the years 1932–7: within this period fell the severe drought of 1932–5.

THE SOIL

Information about the soil is presented under three headings: (*a*) the soil profile, (*b*) chemical data from 6 in. (0–15 cm.) surface samples, and (*c*) data from 1·5 in. (0–3·8 cm.) surface samples.

(*a*) *The soil profile*

Two pits at least were dug in each type and in some types several. From the figures (Fig. 1) and the descriptions it will be seen that we are not dealing with a set of intact profiles. A is maintained immature by erosion as is clear from the pitted surface and the flint covering (Pl. 3, phot. 1). B is the nearest approach to an undisturbed profile, although it is suspected that some contamination from the deposition of blown sand has taken place and that in parts of the area cultivation at some date has occurred—this despite the tradition that Lakenheath Warren has never been cultivated. The evidence for this suspicion is the presence of low enclosing banks set at right angles, the softer state of the surface soil within the enclosed areas and the altered abundance of the species, although the flora remains the same. This conclusion also holds good for parts of C where in addition a reversal of the $CaCO_3$ gradient is found in one profile, although this may well be due to the activity of moles which incidentally are few. Profiles D–G are all overlaid by a blanket of blown sand.

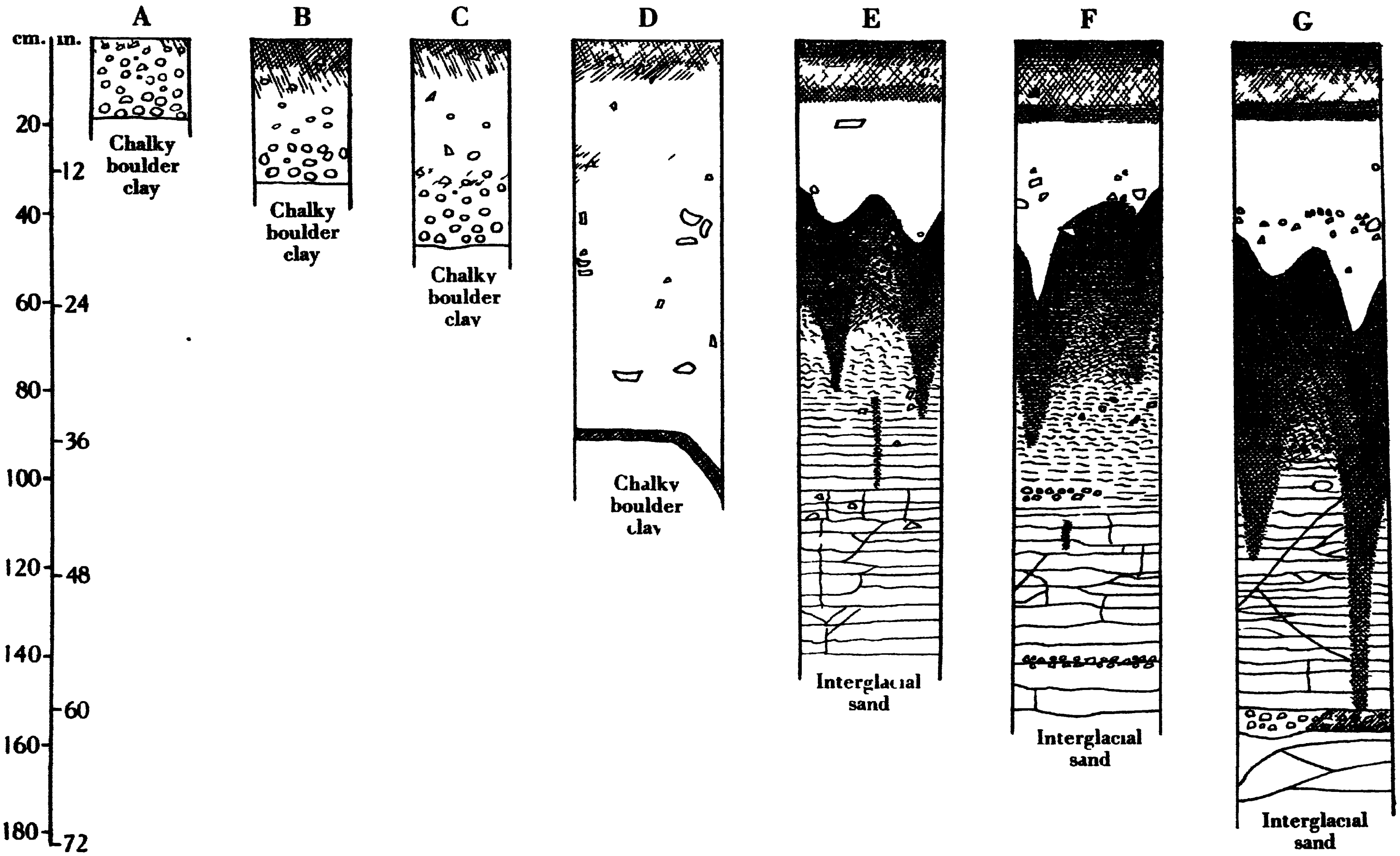

Fig 1 Profiles of the soils of the grassland types studied for description see text, p 45

Descriptions of the soil profiles

Grassland type	Soil horizon	Depth in cm.	
A	A	0–19	Grey with numerous chalk stones, increasing in number and size downwards. Consistence rather earthy.
	C	19–	Compact chalky boulder clay.

In the 14 plots the average depth of soil over the chalky boulder clay is 19 cm. with a range from 13·5 to 27 cm.

B	A	0–18	Medium dark-coloured soil with occasional flints and small chalk stones.
		18–33	Chalk stones increasing in size and number downwards set in a rather earthy matrix.
	C	33–	Compact chalky boulder clay.

In 17 plots the average depth of soil over chalky boulder clay is 33 cm. with a range from 28 to 47 cm.

C	A	0–13	Slightly bleached sand grains at the surface: the whole is coloured by humus. Small chalk stones rare and flints occasional.
	[B]	13–28	Reddish brown, the colour deepening downwards: occasional flints and chalk stones.
		28–46	Numerous chalk stones in earthy matrix.
	C	46–	Compact chalky boulder clay.

In 15 plots the average depth of soil over chalky boulder clay is 46 cm. with a range from 32 to 62 cm.

D	A 0	0–13	Relatively fresh sand with occasional flints.
	A	13–25	Paler sand with occasional flints.
	B	25–38	Slightly purplish in colour; flints scattered.
		38–49	Fawn sand: many flints.
		49–74	Lighter coloured sand with scattered flints.
		74–80	Dark red-brown sticky plastic band.
	C	80–	Compact chalky boulder clay: surface very uneven, deep pockets of sand penetrating the boulder clay.

In 3 pits the average depth of the chalky boulder clay first reached is 84 cm. with a range of 80–92 cm. But there are deep sand pockets in the boulder clay.

E	A 0	0–12	Dirty coloured sand: small flints occasional.
	A 1	12–17	Dark, humus-coloured.
	A 2	17–38	Grey, with occasional flints.
	B	38–	Upper limit undulating. The uppermost 10 cm. is dark purplish brown, consolidated, and projects downwards to at least 1 m. in the form of inverted cones, the cores of which consist of extensions of the A 2 horizon. Between the cones the soil is still consolidated, dark brown and mottled with a network of close-set narrow vermiform dark bands which are replaced lower down by continuous horizontal, oblique and vertical bands of humus accumulation which become more distinct (and more widely spaced) as the background of sand becomes lighter in colour (and looser) with increasing depth. At 2 m. the sand is yellow and quite unconsolidated. There are numerous flints in the topmost layer of B. From the surface to 107 cm. the sand is unstratified: below, to at least 1·8 m., it is distinctly laminated with occasional bands of flints and rounded pebbles. The chalky boulder clay was reached with the borer at 1·9 m.
F and G	—	—	In all essential features profiles F and G are similar to E, differing mainly in the degree of podsolization. The A 2 horizon is whiter and thicker; the upper B horizon is also thicker and more consolidated, and the cones descend to greater depths. In F the bedded sand begins at 117 cm. from the surface, in G 102 cm. Chalky boulder clay was reached with the borer at 2·5 m. in F: in G it was not reached at 3·6 m.

The full profile down to the chalky boulder clay was not exposed in E, F and G, but in E and F it was reached by the soil borer. Now profiles A–D represent a genetically related series whose development can be explained by progressive decalcification of the chalky boulder clay to different depths. The data for profiles A, B and C have already been presented (Watt, 1936): in D the process of decalcification has gone further, and in the residual soil above the chalky boulder clay only the narrow red sticky band contains $CaCO_3$ (0·38 %) (Fig. 2). None of these profiles (A–D) shows stratification in the sand, but in E–G the upper 40 in. (100 cm.) or so rest on laminated sand, interglacial in origin, this in turn resting on chalky boulder clay in E and F and presumably in G as well. The upper 40 in. represents upper chalky boulder clay in which decalcification is complete, the porous laminated sand below facilitating the process. At the same time it ought to be mentioned that in other parts of Breckland podsols similar in development to E, F and G, have been found resting on chalky boulder clay, and in all likelihood derived directly from it.

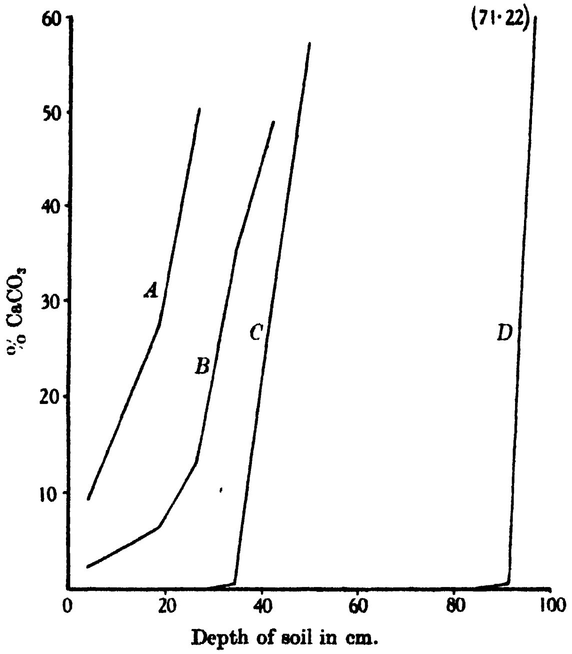

Fig. 2. The distribution of the $CaCO_3$ in the profiles of the soils of grasslands A–D. (N.B. The graph for C is not the same as the one previously given (Watt, 1936): the one given here is more nearly typical of C.)

Mechanical analyses of samples taken at successive 3 in. (7·6 cm.) intervals throughout the profiles in A, B and C and in the different horizons of D, E, F and G show the sandiness of these soils. Apart from samples containing

$CaCO_3$ all show coarse and fine sand fractions of from 85 to 98%: silt is negligible—the highest value is 3·47% and the average 1·29%: the average for clay is 1·34% with values varying between 0·10 and 2·62% if we except the red-brown sticky layer in D which contains as much as 12·09%. In the carbonate-containing samples similar values to those given are found when allowance is made for the $CaCO_3$.

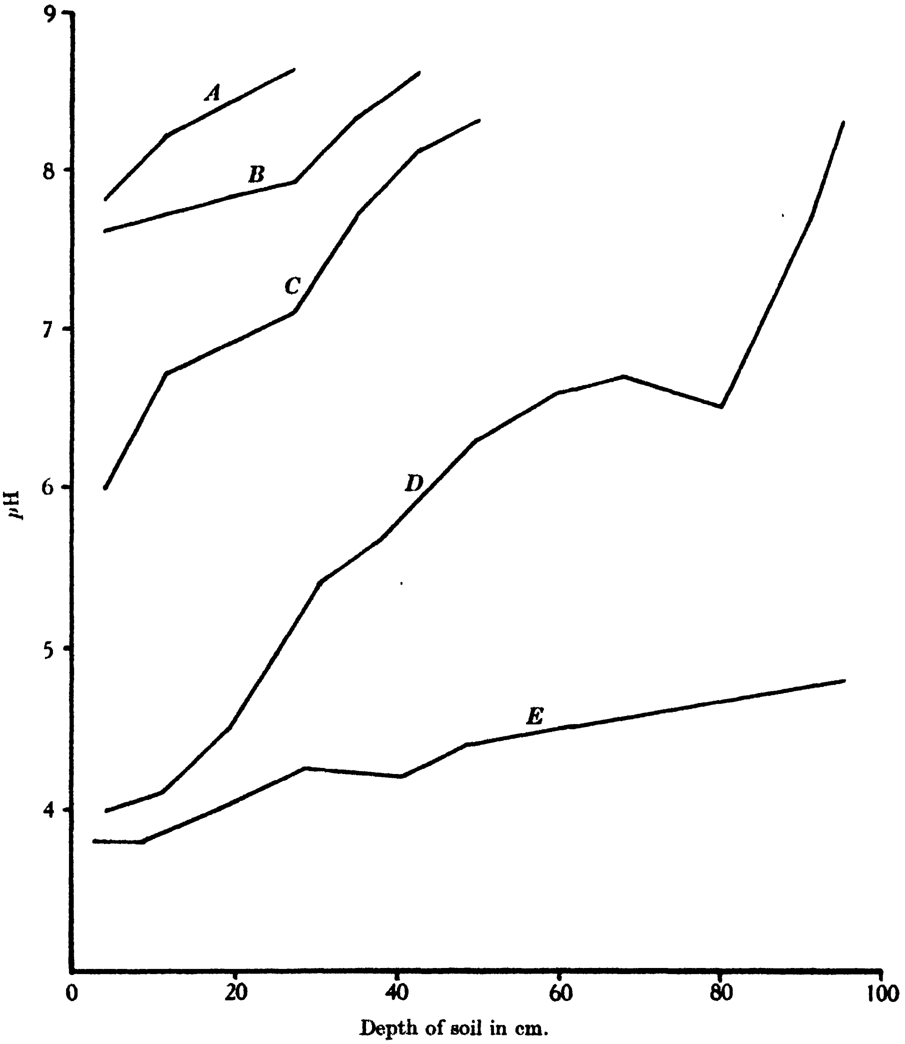

Fig. 3. The *p*H profiles of the soils of grasslands A–E: those for F and G are similar to E.

The removal of the $CaCO_3$ in these clay-deficient soils is followed by a rapid change in the hydrogen-ion concentration. The data for profiles A–E are graphed in Fig. 3: the graphs for F and G are practically identical with that for E and are not given (and the same holds good for the carbon and sesquioxides distribution, *vide* below). The graphs show a progressive increase in acidity in the surface soil of A–E, and in each profile a progressive decrease from the surface downwards. The high acidities in E (and F and G) are noteworthy.

The distribution of carbon (determined by the wet combustion method) is shown graphically in Fig. 4. The graphs show fairly steep but uniform gradients in profiles A and B, a flattening out from C to D and in E (F and G) a sharp contrast between the high values in the surface soil horizons and the lower values at greater depths. Actually in E, F and G dark humus-stained bands occur down to the lowest depths exposed, to 2 m. in G. The curve for E shows two soil horizons with high values for carbon, one in the present surface the other in the surface of the buried profile: F and G repeat this feature.

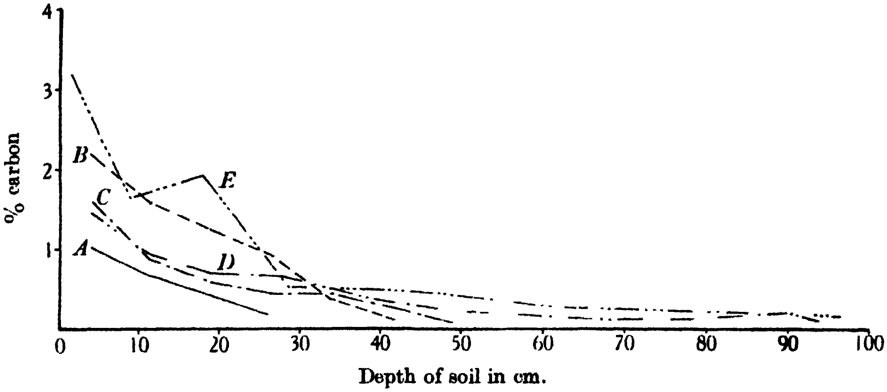

Fig. 4. The "sesquioxides" profiles of the soils of grasslands A–E: those for F and G are similar to E.

The mobilization and transport of the sesquioxides (extracted in conc. HCl) are shown in Fig. 5. The graphs show the progressive removal of the sesquioxides from the upper soil layers and their accumulation (first hinted at in C) in the lower, but the amount in the upper parts of the B horizons is never large: only immediately above the chalk-containing layers is there any considerable accumulation.

Profile D has a blanket of relatively unbleached sand overlying a profile near to a brown forest soil: E, F and G show both in the field and in the analyses a podsol in different stages of development covered by a layer of blown sand which is itself bleached.

These data show that we are dealing with a graduated series of soils of increasing depth with a very immature highly calcareous profile at the one extreme and a well-developed podsol at the other. But the steps in the series are not equal: from A to E the steps are well marked, but F and G differ only slightly from E.

(*b*) *Chemical data from the* 6 *in.* (0–15 *cm.*) *surface samples*

The conclusion just reached on the basis of field observations and analyses of the soil profiles is confirmed by the tests on the composite samples (Table 1, p. 50). The data for the *p*H (checked by Kuhn's colorimetric method), $CaCO_3$ content and exchangeable bases show a gradient of base status, the rapid removal of bases from the surface soil following decalcification and the essential identity of E, F and G. The continuity of the increase in carbon content is interrupted by C (whose relatively low value may be significant), but the nitrogen content does not run *pari passu* with the humus content so that the ratio of carbon to nitrogen while increasing from A to G shows a more rapid rise from D to G than from A to C. This points to a difference in the type of humus formed, a change in fact from the mull type in A, B and C to the highly dispersed acid humus of E, F and G.

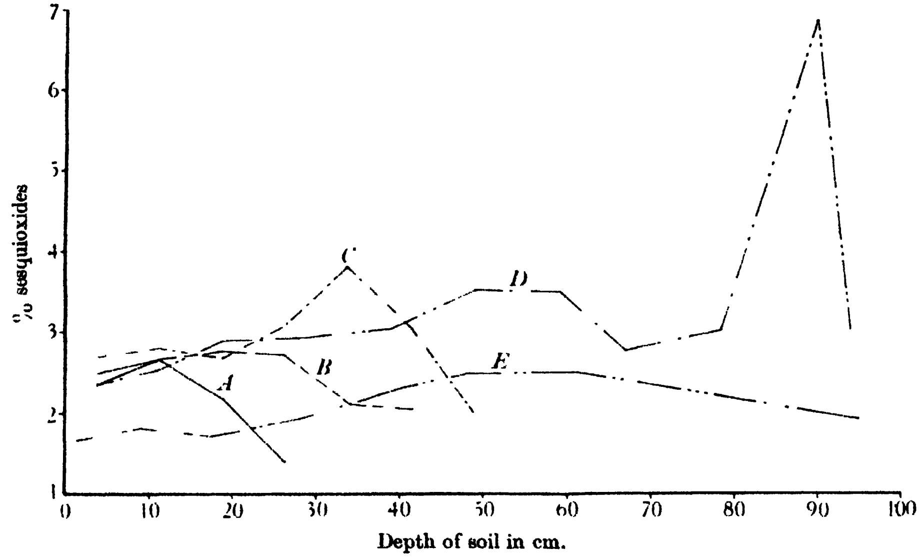

Fig. 5. The carbon profiles of the soils of grasslands A–E: those for F and G are similar to E. Note the high carbon content at about 20 cm. depth in E indicating the level of the buried surface.

(*c*) *Chemical data from the* $1\frac{1}{2}$ *in.* (0–3·8 *cm.*) *surface samples*

The data in Table 1 are values obtained from composite samples which reveal nothing about the range of each within each grassland type. This information has been obtained from the surface $1\frac{1}{2}$ in. (0–3·8 cm.) of soil for the hydrogen-ion concentration and the $CaCO_3$ content (Table 2). The average values for "loss on ignition" for the surface and subsurface samples are also given. The tests were made on composite samples from five samples from each plot. From each grassland type there is therefore a minimum of fourteen values.

The individual *p*H values are set out in descending order within each type in Fig. 6. The plotted points show that within each type the range of acidity is narrow except in C where it is wide. The form of the curve is evidently explicable in terms of decalcification and rapid leaching in a soil deficient in buffering clay.

Table 1. *The results of tests on the* 6 *in.* (0–15 *cm.*) *composite samples from grasslands A–G*

Grassland type	A	B	C	D	E	F	G
*p*H (hydrogen electrode)	8·20	7·81	6·18	4·36	3·95	3·77	3·70
$CaCO_3$ %	17·04	1·61	0·13	0·00	0·00	0·00	0·00
Exchangeable Ca in M.E.	51·20	34·37	6·29	0·76	0·13	0·07	0·06
Total exchangeable bases	75·75	37·90	6·95	1·66	1·10	0·88	0·80
Carbon %	0·900	1·235	1·138	1·275	1·440	2·363	3·15
Total nitrogen %	0·062	0·080	0·070	0·070	0·075	0·094	0·108
C/N	14·51	15·43	16·25	18·21	20·53	25·12	29·16

Table 2. *Average values and the range of values for* pH *and* $CaCO_3$ *in the surface* 1½ *in. of soil: also the average values for "loss on ignition" on the surface* 0–1½ *in. and the* 1½–3 *in. samples*

Grassland type	A	B	C	D	E	F	G
*p*H (Kuhn):							
Average	8·03	7·53	5·96	4·08	3·64	3·78	3·67
Range	7·9–8·2	7·0–7·7	5·0–7·1	3·8–4·7	3·5–3·8	3·6–3·9	3·6–3·8
$CaCO_3$ %:							
Average	12·90	0·79	0·023*	0·00	0·00	0·00	0·00
Range	20·18–5·73	3·82–0·003	0·033–0·000	—	—	—	—
Loss on ignition:							
0–1½ in.	2·55	5·05	4·70	4·19	5·30	7·93	7·52
1½–3 in.	—	4·17	3·47	2·75	2·66	4·83	4·48

* $CaCO_3$ present in two plots only.

The differences in *p*H between A and B are relatively small, but the values for $CaCO_3$ are sharply contrasted, A containing an average of 13% with a minimum of about 6%, B 0·8% and a maximum of approximately 4%. In C only two out of fifteen plots contained any free $CaCO_3$: the rest had none.

The "loss on ignition" values show a general increase from A to F (the smaller amount in G is doubtless due to the fact that about one-half of the samples were collected from soil patches denuded of vegetation): but again it will be noted that the values for C and D are less than that for B and that D has a lower value than C. Comparison between the surface and subsurface values brings out the significant fact of the increase in the differences between them from B to G. No subsurface samples were collected from A.

The soils, then, represent a series of steps in the genesis and development of a podsol, and the various tests applied show increasing acidity and decreasing base status from the most immature to the most mature profile. At the same time the soil depth increases, and this together with the amount and kind of humus is likely to influence the soil-water relations. No data, however, have been obtained on this point.

ANALYSIS OF THE FLORA AND THE VEGETATION

Brief physiognomic characterization of grasslands A–G

The "grass-heath" shows marked variation in physiognomy and floristic composition: in one place there is lichen-heath dominated by *Cladonia silvatica*, in another a floristically rich Breckland variant of chalk pasture. A few species, notably *Agrostis canina*, *A. tenuis*[1] and *Festuca ovina*, are common to all types, and they form the background in a picture where the changing pattern is due to the kind and abundance of their varying associates.

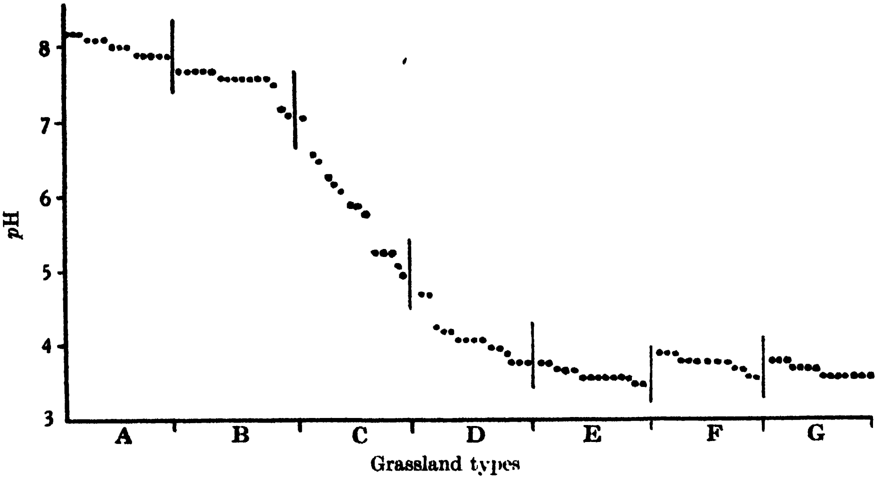

Fig. 6. The pH determinations on composite surface (0–3·8 cm.) soil samples from each plot in grasslands A–G set out in descending order of magnitude within each type.

On the extreme habitat of grassland A the vegetation fails to form a complete cover. The surface is pitted: little hummocks of chalky soil crowned by fescue rise 2–4 cm. above shallow troughs covered with flints and chalk stones and occupied by a fleeting population of ephemerals. Grassland B closely resembles chalk pasture: there is similar floristic wealth and continuity of turf, but the turf is thinner and not so soft. The aspect during early summer is gay with many coloured flowers—purple with *Astragalus danicus*, pink and white with *Thymus serpyllum* and *Asperula cynanchica*, orange with *Lotus cornicu-*

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[1] Samples of *Agrostis* were collected from rabbit-proof enclosures in each grassland type and kindly identified for me by Mr Hubbard of Kew. *A. tenuis* Sibth. and *A. canina* L. were identified from all types. *A. canina* L. var. *arida* Schlechtd. was recorded from A, B, F, G and the *f. mutica* from A, B, C, D, E.

latus, white with *Linum catharticum*, and in August starred with *Sagina nodosa*, all set against a grassy background in which *Festuca ovina* does not form tussocks but has a diffuse habit. Grassland C, in some respects, is B without the large calcicolous element, but the turf is more grassy, somewhat coarser and includes calcifuges. The turf is again continuous except where (as also in B) it is broken by the activities of moles and rabbits, but a significant pointer to interruption in continuity is found in the changing behaviour of *Cladonia silvatica*. In B, *Cladonia* is abundant, but as "individuals": in C it has in general the same habit but occasionally is gregarious, forming small pure patches under which the remains of higher plants are found. In D, these patches of *Cladonia* are larger and more numerous, and the prevailing colour is a blend of the grey of the lichen and green of grass with fescue forming closely grazed flat broad cushions. The part played by lichens increases still more in E, F and G where they determine the prevailing grey colour of lichen heath with scattered compact closely grazed tussocks of fescue, patches of *Agrostis* spp. and large patches of diffuse *Galium saxatile* in E and F, relieving the monotonous grey in June with their abundant white flowers. In E and F the lichen mat is almost continuous, but in G it is broken down in many places and all stages of disintegration to bare soil and building up from it are found. In D–G the lichen carpet conceals the dead remains of higher plants.

This brief outline shows at once a relationship between physiognomy and soil type. The floristic details throw the differences into greater relief.

Interpretation of the lists of species and their abundance

The lists of species should be interpreted with certain qualifications in mind. They have been recorded from a total area which is a small part of Breckland and that area is confined to Lakenheath Warren. Many species local in Breckland and characteristic of certain soil types are not found there, e.g. *Hippocrepis comosa* and *Helianthemum chamaecistus*, both on soils of the B type. *Cirsium acaule*, rare and local on Lakenheath Warren, is abundant in some other places.

Again, while the primary factor differentiating the grassland types is the soil, rabbits appear to play an important part in determining the floristic composition of any one type. Intensive grazing doubtless excludes certain species, alters the relative abundance of others, and allows the entry of a third group. Ungrazed B, while easily recognized as a B type, includes species like *Achillea millefolium*. *Avena pubescens*, *Poterium sanguisorba*, *Scabiosa columbaria* and *Silene otites*, none of which is found on the intensively grazed Lakenheath Warren. *Bromus erectus*, too, has so far been found only in ungrazed areas. Others, like *Avena pratensis* and *Plantago lanceolata*, are much more abundant in ungrazed B, while many annuals of the grazed areas are absent. In this connexion the "continental element" and its distribution within Breckland is of particular importance, but until more critical work is done it is premature to assign its members to their respective grassland types. And, of course, there are other soil habitats than those described in this paper.

Another point of primary importance must be kept in mind, a point which emphasizes the habitat of Breckland as marginal for some species and reduces the usefulness of the quantitative relations of the species in the characterization of the plant communities. Because of yearly variation such records have a limited validity, an observation which is true but without practical significance for many communities but of real significance in Breckland. Thus it is relevant to state that over the period 1932–6 the annual rainfall varied much: it was subnormal from 1932 to August 1935, after which to the end of 1936 it was high for the area. Moreover, the years preceding 1932 were also wetter than usual. The result is that grassland B was listed in a year (1932) when the vegetation was luxuriant (and more luxuriant than it has been since), grassland A within the dry period (1933), and the other types towards the end of the dry period and in 1936 before the vegetation had recovered from the effects of the drought. The drought seriously affected many species: some died out wholesale leaving a few scattered representatives, the abundance of others declined markedly and flowering was much restricted. Thus in 1932 grassland G was traversed, and the notes made record the presence of many large live tussocks of *Festuca ovina* which in a few places almost covered the ground. All these had died by 1936, and the dead tussocks confirmed the earlier record. A similar mortality was observed among *Dicranum scoparium*. Small plants of both these species survived. Again, in 1932, in grassland B *Asperula cynanchica* flowered freely: in 1934 and 1935 flowering was sparse and the return to the 1932 standard did not take place until 1937, i.e. nearly two years after the drought broke. Similar fluctuations are found in the numbers and in the flowering of *Rumex acetosella*- in some years flowering is so abundant as to impart a red colour to the community, in others flowering is negligible. Unfortunately, no counts were made at the beginning of the drought, but the following data for 1935–8 inclusive from a type of "grass-heath" not described here substantiate the above observations. For these years the number of shoots of *Agrostis* spp. per sq. m. are respectively 2320, 870, 3004 and 2344, for *Rumex acetosella* 263, 1299, 276 and 53, and of flowering shoots of this species for 1936–8, 249, 56 and 0. Similar data have been obtained for species unpalatable to rabbits and for species inside rabbit-proof enclosures. Explanations of this phenomenon in terms of varying intensity of rabbit grazing are thus ruled out. It ought to be mentioned that some species are not appreciably affected, and of those which are the degree and extent vary as well as their rate of recovery.

For these reasons then, namely, the localization of certain species, the differences in floristic composition between grazed and ungrazed grassland and the variation in the abundance of certain species from year to year, the need for caution in the interpretation of the data is manifest. Thus the absence of a species from the lists does not necessarily mean an absence from Breckland or from any type, in particular from ungrazed areas, where on ecological grounds a species might be expected, and the data in the lists are qualified in the text where a wider (but still limited) experience dictates. For the same reasons no serious attempt is made to compare and correlate these grassland types with other similar types in this country and on the continent. The ecology of the "continental element", the influence of rabbits (enclosures have been made in all the grassland types) and the fluctuations in numbers are subjects of special studies: when these are completed comparison and correlation will then be more illuminating.

Ecological relationships of the flora

The lists of species and the tabulation of their numbers in each type (Table 3*a*) show the great variation in floristic wealth. Out of a total of ninety-two species of vascular plants from all types taken together there is a maximum in B with 80 and a falling away from it on either side, to 50 in A and through a descending series to 9 only in G. The bryophytes fall into the same kind of series with maxima in B and C and a minimum in G, although the range in number is not so great. The number of species of lichen is much more uniform with a slight maximum in A.

Table 3. *The numbers of vascular plants, bryophytes and lichens in each type separately* (*a*) *and in fractional groupings* (*b*)

	a							*b*						
Grassland type	A	B	C	D	E	F	G	A–G	B–G	C–G	D–G	E–G	F–G	G
Vascular plants—all species	50	80	59	37	22	16	9	92	86	61	38	23	16	9
Vascular plants—annuals	20	31	22	13	10	6	2	36	34	25	14	10	6	2
Bryophytes	10	31	32	15	11	12	8	42	40	33	16	12	12	8
Lichens	15	11	12	12	13	12	12	24	19	17	15	14	13	12

The distribution of the species among the types shows that nearly all species found in two or more types have a continuous range in serially contiguous types: a few only are discontinuous. Table 3*b* gives the total numbers in a progressively eliminating series. It is clear that B provides the most suitable habitat for the majority of the species and different factors are at work causing a gradual elimination of the less tolerant and not a radical change in the species composition. Thus in B–G (taken together) there are eighty-six species of vascular plants or only six more than in B alone: in C–G, sixty-one, two more than in C alone, the differences being one only in the next two sets compared. In other words the species of the podsolized soils are mainly those tolerant of a wide range of soil conditions. The data for the bryophytes show the same kind of fractional separation: the lichens, on the other hand, show a proportionately greater change in species composition. It is interesting to note that the annuals (and the perennials) when treated as a separate group show the same kind of quantitative distribution as the vascular plants.

On the basis of soil preference the species may be conveniently classed into four groups without hard and fast lines between them: tolerant, exacting, calcicole, calcifuge. Tolerant species are found in all seven types and are best exemplified by *Agrostis canina*, *A. tenuis*, *Festuca ovina*, *Hypnum cupressiforme*, *Cetraria aculeata*, *Cladonia furcata* and *C. pyxidata*. *Aira praecox* and *Luzula campestris*, rather restricted in A to more sandy places, may also be included here. Exacting species (usefully subdivided into more and less exacting species) have a narrower range beginning in A or B, generally reaching maximum values for constancy and abundance in B and C and with reduced values in D (more exacting) or maintaining significant values in D and stopping there or tailing off thereafter to end in E, F or even in G as non-significant plants (less exacting). Representative examples of the more exacting are *Arenaria tenuifolia*, *Carex ericetorum*, *C. praecox*, *Cerastium arvense*, *Draba verna*, *Koeleria gracilis*, *Bryum roseum*, *Climacium dendroides*, *Hylocomium rugosum*, and of the less exacting *Alchemilla arvensis*, *Campanula rotundifolia*, *Cerastium semidecandrum*, *Galium verum*, *Hypochaeris glabra*, *Senecio jacobaea*, *Brachythecium albicans* and *Cladonia rangiformis*. Calcicoles form a large and important element in A and B, much less so in C where they are local, rare or have a low constancy and average abundance. Calcifuge species make their first appearance in those B plots which show an approach to the C type and increase in importance thereafter. *Teesdalia nudicaulis*, *Rumex acetosella*, *Galium saxatile* (first appearance in C), *Cephaloziella starkii*, *Ceratodon purpureus*, *Hypnum schreberi*, *Polytrichum juniperinum*, *P. piliferum*, *Ptilidium ciliare*, *Biatora granulosa* and *B. uliginosa*—the last two on the more acid soils only.

The number of the acidiphilous species is small, and the interesting fact is not their appearance as the soil becomes suitably acid but their small number. The usual acidiphilous flora of acid soils is little more than represented: common species like *Deschampsia flexuosa*, *Nardus stricta*, *Erica cinerea*, *Potentilla erecta* and *Vaccinium myrtillus* are absent from the lists, and while some of these do occur in Breckland, most play a minor part. For *Nardus* and *Deschampsia*, Jeffreys (1918) suggests grazing by rabbits and dryness of the habitat as restrictive factors, and, as we have already seen, the periodic shortage of water is a likely explanation of the difficulties experienced by plants in holding their own and spreading.

Between A and B water is also the probable differentiating factor, only the less needy surviving in A, although the high $CaCO_3$ content may also be a directly operative factor.

Life-form. Biological spectra

Drought-resistant and drought-evading species compose these grasslands. On the whole the individual plants are small (and practically all have small, narrow or folded leaves) although there is variation in vigour as well as in number of individuals (or shoots) and in flowering from year to year.

Table 4. *Biological spectra of grasslands A–G separately and of all species taken together*

Life form	Ch.	H.r.	H.s.	H.c.	G.r.	G.rad.	T.	Totals
Grassland A	1 (2)	8 (16)	13 (25)	6 (12)	2 (4)	1 (2)	20 (39)	51 (100)
„ B	9 (11)	7 (8·5)	20 (24·5)	10 (12)	3 (3·5)	2 (2·5)	31 (38)	82 (100)
„ C	9 (15)	8 (13·5)	10 (16·5)	6 (10)	3 (5)	2 (3·5)	22 (36·5)	60 (100)
„ D	5 (13)	5 (13)	6 (16)	5 (13)	2 (5·5)	2 (5·5)	13 (34)	38 (100)
„ E	1 (4·5)	2 (8·5)	5 (21·5)	4 (17·5)	0 (0)	1 (4·5)	10 (43·5)	23 (100)
„ F	1 (6)	1 (6)	4 (23·5)	3 (17·5)	1 (6)	1 (6)	6 (35)	17 (100)
„ G	1 (10)	1 (10)	2 (20)	3 (30)	0 (0)	1 (10)	2 (20)	10 (100)
All species grasslands A–G	11 (12)	9 (9·5)	22 (23·5)	10 (10·5)	4 (4·5)	2 (2)	36 (38)	94 (100)

The high number of annuals is the important feature of the spectra (Table 4). The hemicryptophytes are correspondingly low. The spectrum is in fact the best single physiognomic criterion emphasizing the difference in conditions (including plant competition) between the "chalk pasture" of the South Downs (Tansley & Adamson, 1926) and the "grass-heath" of Breckland. Now the spectrum for all species taken together is practically identical with that for grassland B, the additional twelve species being distributed in such a way as to leave the proportions practically unchanged: and grassland B, floristically and physiognomically the nearest approach to chalk pasture, has 38 to 13% T. for chalk pasture and only 45% H. as against 72% H. for the latter community. The reduction in number of hemicryptophytes is absolute as well as relative, brought out clearly in the important group of the grasses. In chalk pasture there are twenty-five species, in grassland B fifteen only: fourteen are not found in B (including one annual *Bromus mollis*) and ten are common to both, and of the five additional in B (*Agrostis canina*, *Aira caryophyllea*, *A. praecox*, *Festuca myuros*, *F. rigida*), four are annuals. These two life-form classes make up the bulk of the spectrum. The other two classes show complementary differences: chalk pasture has only 5% Ch. to the 11% Ch. of grassland B, to which only *Cerastium arvense* is peculiar, but it has 10 to 6% G. in grassland B. This higher percentage of geophytes in chalk pasture is due to the inclusion of orchids, none of which is found on Lakenheath Warren: on the other hand, the Breckland figure includes another species of limited range, namely, *Carex ericetorum*. Mention ought here to be made of the geophyte *Botrychium lunaria* (exclusive to grassland A) which is not found in chalk pasture.

Comparison between the spectra for the different grasslands is rendered difficult by the unequal number of species and especially by the low numbers in E, F and G. The fractional elimination of species, attributable to their soil requirements, applies to all life-form classes although in different degree. Apart from the annuals perhaps the most striking is the variation in actual numbers of chamaephytes, there being one only in each of A, E, F and G and nine in B and C. Among the hemicryptophytes the scapose subclass contains a higher number than might have been expected, but apart from the ruderal *Urtica dioica* none has large leaves and ten out of twenty-two for all species are in fact partial rosette plants.

The form of *Festuca ovina* is of interest. At the extremes, in A and especially in E, F and G, *F. ovina* is a close-set tufted plant and this form becomes progressively more diffuse as B is approached: in the continuous floristically rich sward of B the tufted form is lost.

All species, irrespective of their values for abundance and constancy, have been used in computing these spectra, but spectra based on species with high constancy and high average abundance (Table 5) reveal similar major groupings. Those for all the grassland types taken together are almost identical: those for A, B, C and D taken separately reveal non-essential differences, the therophytes and hemicryptophytes having values of similar magnitude to those for the spectra of all species. In E, F and G the significant species are the same, and although the validity of observations on spectra based on so few species may well be questioned, the therophytes still remain fairly high and the hemicryptophytes relatively low. Incidentally, the caespitose hemicryptophytes in E, F and G are more numerous than the scapose forms.

Table 5. *Biological spectra computed from species with constancy* 4 *and* 5 *and/or average frequency of* 2·1 *and over of each grassland type and of all taken together*

Life-form		Ch.	H.r.	H.s.	H.c.	G.r.	G.rad.	T.	Total (100)
Grassland	A	1 (4)	3 (12)	4 (15)	4 (15)	1 (4)	1 (4)	12 (46)	26 (100)
,,	B	5 (12)	4 (9·5)	9 (21·5)	6 (14)	2 (5)	1 (2)	15 (36)	42 (100)
,,	C	5 (14·5)	4 (12)	5 (14·5)	4 (12)	2 (6)	2 (6)	12 (35)	34 (100)
,,	D	1 (5)	3 (14)	5 (24)	3 (14)	0 (0)	1 (5)	8 (38)	21 (100)
,,	E, (F, G)	1 (11)	1 (11)	1 (11)	3 (33)	0 (0)	1 (11)	2 (22)	9 (99)
,,	A–G	7 (12)	5 (9)	11 (19·5)	6 (10·5)	3 (5)	2 (3·5)	23 (40·5)	57 (100)

Seasonal aspects

The perennial grasses, evergreen herbs and the lichen mat of *Cladonia silvatica* form in the different types a little changing background relieved for longer or shorter periods by bursts of flowering. In the grazed pasture of Breckland as a whole it is the annuals which attract attention: many germinate in autumn, survive the winter as rosettes, and vegetate and flower freely to set seed and die before the middle of July. They come away at a time of the year when rabbits have more than they can eat, but their escape is in part due to their unpalatability and the early-flowering *Draba verna* and the late-flowering (drought resistant) *Galium anglicum* appear to escape for this reason. On the flowering of palatable perennials grazing by rabbits is in no example better seen than in *Galium verum* whose free flowering in some enclosures presents such a striking contrast to the almost flowerless grazed pasture. Grasses are, of course, obviously affected in this way, but *Campanula rotundifolia*, *Carlina vulgaris*, *Rumex acetosella*, *Botrychium lunaria* (eaten almost as soon as it emerges in April: in the enclosure sporing freely in June and July) and many others suffer, and were it not for their perennation and their ability to reproduce vegetatively would in time disappear.

Despite the score of annuals in grassland A the general background is little affected because the relatively few individuals are small and have small flowers. None is really showy except the occasional *Calamintha acinos*. The perennials with larger flowers produce no striking effect, partly because of their low frequency, partly because of grazing but largely also because of the unfavourable habitat, for in the enclosure the general aspect is much the same as outside, even *Festuca ovina* flowering sparingly only.

It is in grassland B that flowering is most obvious, beginning in April or even at the end of March with *Carex praecox* and *Draba verna* and ending with the flowering of *Sagina nodosa* until late in August. In the pageant of flowers the annuals generally come first, the perennials later: most of the flowering of the annuals is concentrated in May overruning into June or even later (*Cerastium semidecandrum*, *Myosotis collina*, *Saxifraga tridactylites*, *Veronica arvensis*): *Arenaria serpyllifolia* and *A. tenuifolia* flower from May to July and the showy *Linum catharticum* in June and July, when it is reinforced by the perennial *Asperula cynanchica.* Also at this time come the purple-flowered *Astragalus danicus* and *Thymus serpyllum* (many with white flowers) and the yellow *Lotus corniculatus*—all with stragglers as late as the end of August.

In grassland C many of the species which give colour to B are rare (*Astragalus*, *Linum*, *Sagina*) or local only (*Asperula*, *Thymus*), and the white of the patchy *Galium saxatile* in June is a small and brief compensation. The general tone is affected only slightly by the early spring annuals.

The prevailing green of C is replaced in E, F and G by the drab grey of *Cladonia silvatica*: D is intermediate, patchy grey-green relieved for a brief period by the white flowers of *Galium saxatile*, as also in E, F and G where *Galium* is patchy.

But even in the same type the aspect may vary in some particular from year to year. Mention has already been made of the behaviour of *Asperula cynanchica*, and one or two further examples illustrate the point. In 1932 the grasses of grassland B grew so luxuriantly that flowering was abundant: nothing comparable has since been attained. Again, in June 1933, grassland E was red with flowering and fruiting *Rumex acetosella*: since then *Rumex* has been much less abundant and flowering sparse. And this effect is seen both in palatable and unpalatable species (e.g. *Galium saxatile*), so that variation in the number of rabbits taken by itself is not a tenable explanation. The primary cause appears to be climatic.

The sifting of species on the basis of high abundance and constancy (Table 6) brings out clearly what the soil analyses foreshadowed, namely, that E, F and G are essentially the same. Physiognomically they are alike, and the floristic differences are attributable to the overflowing from D of a few exacting species (*Hieracium pilosella*, *Koeleria gracilis*, *Senecio jacobaea*, *Campanula rotundifolia*, *Galium verum*) with much reduced values for constancy and abundance and to species which are local, often associated with patches of *Urtica dioica* (where the soil is much disturbed by rabbits in search of the rhizomes which they eat during winter and times of scarcity during the summer) and with abandoned rabbit burrows.

Table 6. *The numbers of vascular plants, bryophytes and lichens with constancy 4 and 5 and/or average frequency 2·1 and over in each grassland type taken separately and together*

	A	B	C	D	E	F	G	A–G
Vascular plants, all species	25	41	33	20	8	8	8	55
Vascular plants, annuals	12	15	12	8	2	2	2	23
Bryophytes	7	16	11	12	6	5	6	26
Lichens	10	7	7	9	8	7	7	16

The differentiating species other than those mentioned are mainly annuals, all of which are confined to disturbed soil except *Aira praecox* and *Teesdalia nudicaulis*, which although more commonly found there than elsewhere yet do grow in the continuous carpet of lichen. The moss *Brachythecium albicans* and the lichen *Cladonia rangiformis* are similar differentiating species. The analysis thus shows that there are five major communities of grass-heath with two minor variants on the podsolized soil.

DESCRIPTION OF THE GRASSLANDS A, B, C, D, E, F AND G

Grassland A (list of species, pp. 65–7)

Differentiated by the highly calcareous shallow dry soil, an altogether rather extreme habitat, grassland A is an open community (Pl. 3, phot. 1) characterized by a fairly rich flora including some interesting species confined to it. Of these the most important are *Botrychium lunaria*, *Galium anglicum*, the moss *Ditrichum flexicaule* var. *densum* (found occasionally in grassland of the B type) and the lichens *Lecanora lentigera*, *Leptogium subtile*, *L. turgidum*, *Placodium fulgens*, *Psora decipiens* and not given in the list of species, *Bilimbia aromatica* and *Collema tenax*. *Collema* and *Nostoc commune*[1] both show in considerable numbers after wet periods. Other species show a marked preference: *Calamintha acinos*, *Sonchus asper* (seedlings only), the moss *Thuidium*

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[1] Kindly determined for me by Dr V. J. Chapman.

abietinum and the lichens *Biatorina coeruleonigricans* and *Diploschistes scruposus* (also recorded from acid soils, Watt, 1938). *Erigeron canadense*, a notorious and vigorous weed of arable land in the neighbourhood, attaining here a height of a few centimetres only, *Leontodon hispidum*, found also in C and recorded from an ungrazed B, *Plantago coronopus*, very small and local on trodden paths, and *Ranunculus bulbosus*, a rare plant but recorded also as a rare plant in ungrazed B—and the only record of a *Ranunculus* from grasslands A–G—are all found in A.

The physiognomy is determined by the grasses chiefly by *Festuca ovina*, the only higher plant with a high frequency. It forms flat grazed cushions raised 2–4 cm. above the level of the bare soil between them. *Agrostis*—both *canina* and *tenuis*—is occasional only, and many plants exist in a closely tufted form. The rest are never more than occasional or at most locally frequent except *Botrychium*. This plant comes up in April in considerable numbers but is quickly eaten by rabbits, and during spring and early summer a few stragglers only of mature but small (*c*. 3 cm.) plants are seen. *Ditrichum flexicaule* var. *densum* in compact cushions, *Camptothecium lutescens* and *Hypnum cupressiforme* are the only mosses with a frequency higher than occasional. There are no liverworts. Lichens are more noticeable with *Cladonia rangiformis*, *C. furcata* and *Psora decipiens* frequent, *Cetraria aculeata*, *Cladonia alcicornis* and *Placodium fulgens* occasional to frequent, the last in two plots only.

In striking contrast to the small number with high frequency are those with high constancy: almost one-half (twenty-four) of the higher plants have constancy values of 4 or 5, seven out of ten mosses and nine out of fifteen lichens (*vide* lists).

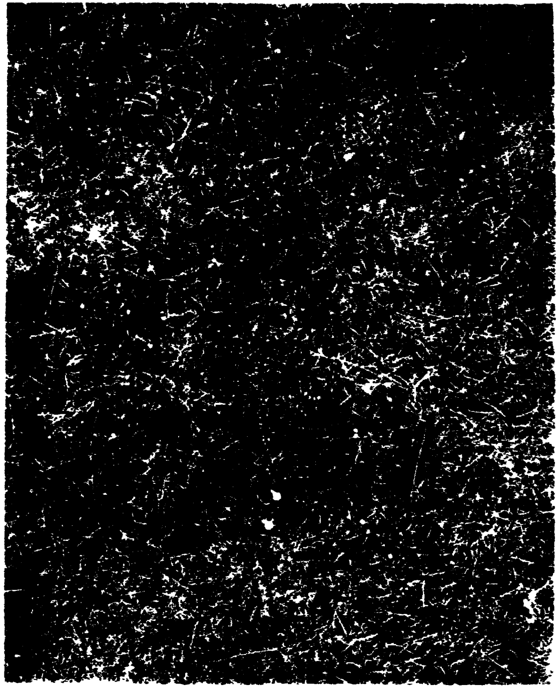
In species the annuals bulk large (39%), and one-half of them have a high constancy. All except *Galium anglicum* are early flowering and are over by mid-July or earlier: *G. anglicum* flowers in July and sets seed in August. It is therefore a drought-resistant annual.

Flowering of the perennials is restricted even in the rabbit-proof enclosure, and shortage of water is probably responsible for this as for the subnormal size of plants with a wider range. Thus *Senecio jacobaea* exists almost entirely in the rosette form (surviving at least three years), and the rare flowering individuals do not exceed about 25 cm.

As is to be expected in a habitat of this kind, calcicoles and the more exacting species make up the greater part of the flora. Among the less exacting and the tolerants the following species are local, largely confined to places where there is more sand: *Alchemilla arvensis*, *Aira praecox*, *Campanula rotundifolia*, *Luzula campestris*, *Myosotis collina* and the lichen *Cladonia silvatica* which occasionally also grows in tufts of grazed fescue.

21 7 33

Phot. 1. Grassland A. Note the discontinuous cover of vegetation and the flint-strewn surface. The most abundant species is *Festuca ovina*. *Koeleria gracilis*, *Senecio jacobaea* and *Psora decipiens* are present.



21 7. 33.

Phot. 2 Grassland B. Note the continuous plant cover made up mainly of *Festuca ovina* and *Agrostis* spp. *Asperula cynanchica*, *Linum catharticum*, *Lotus corniculatus* and *Thymus serpyllum* are in flower.

Grassland B (Pl. 3, phot. 2)

Where the soil in A is deeper, as often round the margins of the patches, fescue tends to form a more continuous turf as in B, but B itself is on the whole sharply defined on the side of A, less so towards C, and four plots included in B show a definite approach to C.

The greater depth of soil, which is still alkaline, presumably means a less widely fluctuating water content through the year than in A. The flora is rich, the richest of all the types forming a short and typically continuous turf. Of the species recorded only from B, *Arabis hirsuta*, *Briza media*, *Cirsium acaule*, *Daucus carota*, *Ononis repens*, *Avena pratensis*, *Anthyllis vulneraria* (the last two also in examples near C) may be mentioned as the others are known to occur in other variants of grass-heath not dealt with here. The mosses *Brachythecium purum*, *Eurhynchium striatum* and *Hypnum chrysophyllum* are recorded only from B. No lichen is exclusive to B.

Of the eighty species of higher plants forty-one have a high constancy and/or a high average frequency. The figure forty-one is made up of fifteen (including ten annuals) with high constancy alone, twenty-two (four annuals) with high constancy and high average frequency and four (one annual) with high frequency. The turf is composed mainly of *Festuca ovina* (in a diffuse form). *Thymus serpyllum* (a.), *Galium verum*, *Koeleria gracilis* (f.-a.), *Agrostis canina* and *A. tenuis*, *Asperula cynanchica*, *Campanula rotundifolia*, *Carex praecox* (usually in large patches), *Carex ericetorum*, *Linum catharticum* and *Lotus corniculatus* generally frequent, but varying from occasional to abundant. All these have a high constancy. Quite a number are occasional to frequent or may even be locally very abundant: *Anthoxanthum odoratum*, *Astragalus danicus* (l.d.), *Cerastium triviale*, *Hieracium pilosella* (often in patches), *Luzula campestris* (rather evenly distributed), *Sedum acre* (usually in broken turf) and *Trifolium repens* (patchy).

In this close turf where as many as eight species may be counted to the sq. in. (6·25 sq. cm.) annuals although rich in species are not markedly rich in individuals: *Linum catharticum*, *Aira caryophyllea* and *A. praecox* are exceptions. Others, like *Arenaria tenuifolia*, *Medicago lupulina*, *Myosotis collina*, and *Veronica arvensis*, seem to hold their own, but *Alchemilla arvensis*, *Draba verna*, *Festuca rigida*, *Saxifraga tridactylites* are more commonly found on disturbed soil.

Grassland B is also rich in bryophytes (thirty-one species) of which one-half (sixteen) have high constancy and/or high average abundance: four have high constancy alone, nine high constancy and high frequency and three have high average frequency alone. On the whole they play an unimportant part, and were it not for the close grazing would play still less. The tolerant *Hypnum cupressiforme* and *Dicranum scoparium* have the highest frequency values. Others less frequent but significant as indicators are *Brachythecium purum*, *Camptothecium lutescens*, *Encalypta vulgaris*, *Eurhynchium megapolitanum*, *Frullania tamarisci*, *Hylocomium rugosum* and *H. splendens*. *Tortula ruraliformis* and *Rhacomitrium canescens* are found here as elsewhere on disturbed soil.

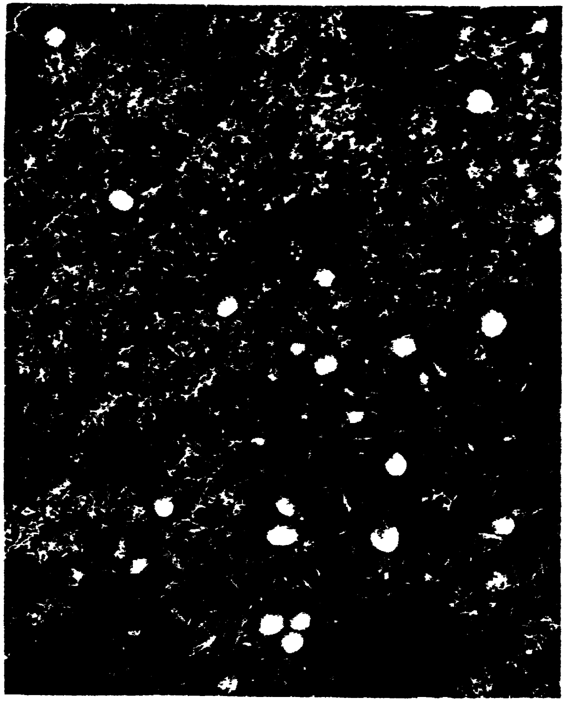
Compared with grassland A the lichens are uninteresting, and of the eleven species one has a high constancy only and six have a high constancy and high frequency. They are found as "individuals" and never in pure patches. *Cladonia silvatica* is the most abundant, and in descending order of frequency come *C. rangiformis*, *C. furcata*, *Cetraria aculeata* and *Peltigera polydactyla*.

Quite a number of species, although not strictly confined to B, are nevertheless characteristic of it, and their occasional occurrence in C usually denotes a local soil variation of the B type. Plants like *Asperula cynanchica*, *Astragalus danicus*, *Linum catharticum*, *Lotus corniculatus*, *Sagina nodosa* and *Thymus serpyllum* are, as shown by their constancy and frequency values, essentially plants of grassland B, although others are found either in A or C or in both. Almost invariably when a digging is made where *Asperula* grows in C the soil is found to be of the B type.

In some places patchiness in the vegetation is evident. There are two obvious causes, one the gregarious growth of *Carex praecox* and the other soil variation. Owing to differences in the structure and proportion of sand to chalk in the chalky boulder clay, the rate of leaching varies from place to place and the result is registered in the vegetation. In the more sandy patches as well as in places where the rate of leaching is slower, but the degree of leaching has reached the same stage as in the patches, acidification of the surface soil is suggested by the presence of *Hypnum schreberi* in particular but also by *Ceratodon purpureus* and *Polytrichum juniperinum*. These herald the change from B to C as do *Rumex acetosella* and *Teesdalia nudicaulis*.

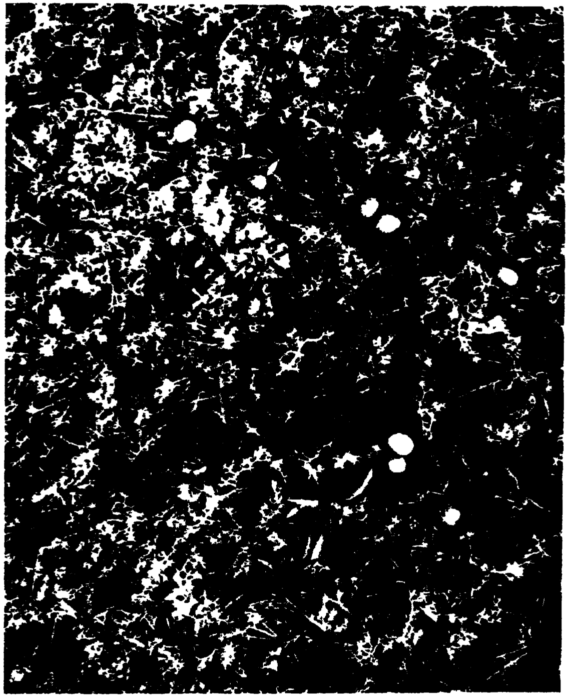
Grassland C (Pl. 4, phot. 3)

Briefly characterized grassland C is B without the stricter calcicoles and with a weak representation of less strict calcicoles and of the more exacting species. Without the dilution due to these sets of species the turf appears more grassy, and in fact *Agrostis canina*, *A. tenuis* and *Festuca ovina* grow more vigorously here than in B and are more abundant. But the abundance of *Campanula rotundifolia*, *Carex praecox* (and probably *C. ericetorum*), *Galium verum* and *Hypnum schreberi* is also characteristic. These features, together with the presence of the calcifuge, *Galium saxatile* and *Webera nutans*, are diagnostically the most important. They are interpretable in terms of the progressive acidification (as described on p. 51 there is a fairly wide range of *p*H), reduction of base status and a deepening of the soil, these changes resulting in a shift of the focal equilibrium in the soil and in the relationships between the species leading to the exclusion of strict calcicoles on edaphic



Phot. A. Burges

Phot. 3. Grassland C. The continuous cover is made up mainly of *Festuca ovina* and *Agrostis* spp. which grow more vigorously than in Grassland B. *Cladonia silvatica* shows a tendency to form aggregates.



Phot. A. Burges

Phot. 4. Grassland F. *Cladonia silvatica* becomes the dominant plant and *Luzula campestris* and *Galium saxatile* (in flower) are scattered through it.

grounds, the reduction in values for constancy and average abundance indicating the tendency towards elimination of the more exacting species and the increase in values the opposite tendency in less exacting and tolerant species.

The net result is a reduction in the total number of species, although the number of bryophytes and lichens remains practically the same. Of the fifty-nine vascular plants, thirty-three, a slightly higher proportion than in A or B, have high values for constancy and average abundance. Fifteen species (including nine annuals) have high constancy alone, and the relatively large number is due to the opportunity for establishment afforded by a vegetational cover broken by rabbits and by the superficial tunnelling of moles: sixteen species (three annuals, *Aira praecox*, *Myosotis collina*, *Veronica arvensis*—one tolerant and two less exacting) have high values in both, and besides those mentioned in the preceding paragraph as diagnostic, *Trifolium repens* is more widespread than in B, while *Luzula campestris* and *Rumex acetosella* are more abundant and *Koeleria gracilis* less abundant than in B. Two species with high abundance are local only, namely, *Asperula cynanchica* and *Cerastium arvense*.

The soil change is reflected in the bryophytic flora. Some species of calcareous soils are still to be found, *Barbula rubella* and *Encalypta streptocarpa* (both rare) and *Camptothecium lutescens*, *Encalypta vulgaris* and *Hylocomium rugosum* with lower constancy or average frequency values compared with B. At the same time *Bryum roseum*, *Ceratodon purpureus*, *Hypnum schreberi*, *Lophozia barbata*, *Polytrichum juniperinum* and *Ptilidium ciliare* show an increase; the tolerants *Dicranum scoparium* and *Hypnum cupressiforme* maintaining high values. Curiously enough *Hylocomium splendens* goes out.

The lichens are not specially characteristic. There are no calcicoles, and the most important features are the increase in *Cladonia silvatica* and its more gregarious habit: occasional pure patches of small size (*c.* 1 sq. dcm.) are found which have below them the dead remains of grasses.

Grassland D

The soil is now fairly deep, very acid, of low base status but to the eye only very slightly podsolized. Calcicoles and the more exacting species are definitely excluded, only the local *Tortula ruraliformis* and *Climacium dendroides* are found in small patches of disturbed soil where also small chalk lumps occur. Thus the less exacting and the tolerant species make up the vegetation.

It is a patchwork of grey and green irregular patches of a quarter of a square metre or more of almost pure *Cladonia silvatica* alternating with similar sized closely cropped cushions of turf made up mainly of *Festuca ovina*. *Agrostis* spp. are on the whole less abundant than in C, but both they and *Festuca* (and *Koeleria gracilis*) grow more luxuriantly in the enclosure than in the enclosure in C. Both *Campanula rotundifolia* and *Galium verum* show a decided drop but still have fairly high values for frequency, maintaining the highest figure for constancy: *Carex praecox* (*C. ericetorum* is absent) and *Koeleria*, on the other hand, drops significantly. In contrast to these *Viola canina* shows higher values here than in any other type; *Luzula campestris* maintains high values in constancy and average frequency, and maintaining the highest values for constancy *Rumex acetosella* and *Teesdalia nudicaulis* increase in abundance, while *Galium saxatile* increases significantly in both.

Of the thirty-seven species twenty have significant values, and nearly all the perennials have both a high constancy and a high abundance. On the other hand, most of the annuals—there are eight of them—have smaller values in constancy and/or average frequency than in C with the exception of *Aira praecox, Teesdalia nudicaulis* and *Hypochaeris glabra.*

The bryophytes may be interpreted using the same general principle. Apart from *Tortula* and *Climacium*, all the species are either tolerant or calcifuge. The majority of the significant species show increases in constancy and/or average frequency, and some have higher values here than in any other type. *Hypnum schreberi* and *H. cupressiforme*, on the other hand, show decreasing values.

None of the lichens found are calcicole, and the most interesting facts relating to them are the first appearance of *Biatora granulosa* and the increasing sociability of *Cladonia silvatica.* Here, too, the removal of the lichen carpet reveals the dead remains of higher plants.

Grasslands E, F (Pl. 4, phot. 4) *and G* (Pl. 5, phot. 5)

For reasons already adumbrated these three types are taken together, forming one type equivalent in status to the others. The podsolized soil is extremely acid and infertile and, when wet, almost black or purplish black in colour although the humus content is not high.

They are characterized by floristic poverty: the real dominant is *Cladonia silvatica* which forms a carpet in which are set scattered tufted *Festuca ovina*, smaller patches of *Agrostis* spp., and larger patches of sprawling *Galium saxatile*, which for a brief period in the middle and end of June relieves the monotonous grey with white. The significant species (all have the highest constancy value) are tolerants and calcifuges only. The other significant species besides those previously mentioned are *Luzula campestris* (o.–a.), *Rumex acetosella* (o.–f.) and the annuals *Aira praecox* and *Teesdalia nudicaulis*, the last two most abundant on bare soil but also growing in the lichen carpet. Like the higher plants all the bryophytes and lichens are tolerant or calcifuge.

Despite essential uniformity, E, F and G differ in points of detail, and the differentiating species suggest a gradation of infertility. First, in the unbroken carpet of lichen, *Hieracium pilosella* (one plant only), *Hypochaeris glabra* and *Senecio jacobaea* (both in four plots only) and *Koeleria gracilis* (one plot only)

Life-form	Grassland type ...	A		B		C		D		E		F		G	
		C.[1]	A.F.[2]	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.
T.	Galium anglicum	3	2·1												
G.r.	Botrychium lunaria	5	2·5												
T.	Erigeron canadense	4	1·8												
H.r.	Plantago coronopus	1	1·0 l.[3]												
H.s.	Ranunculus bulbosus	1	1·0 r.[4]												
H.r.	Leontodon hispidum	3	1·0		—		+								
T.	Sonchus asper. (seedlings)	4	1·3		—	1	1·0								
H.s.-T.	Calamintha acinos	4	1·8	2	1·4										
H.s.	Carlina vulgaris	3	2·0	3	1·8										
T.	Festuca rigida	5	2·0	5	1·7										
H.c.	Holcus lanatus	1	1·0 l.	1	1·0										
T.	Linum catharticum	2	1·5 l.	5	2·7		+								
T.	Medicago lupulina	2	1·0	3	1·9										
H.s.	Prunella vulgaris	1	2·0	2	1·3										
H.s.	Rumex acetosa	1	1·0	1	1·0										
H.s.	Convolvulus arvensis	1	1·0	1	1·0										
H.s.	Anthyllis vulneraria		—	1	1·0										
H.s.	Arabis hirsuta		—	2	2·3										
H.c.	Avena pratensis		—	4	1·9										
H.c.	Briza media		—	2	2·0										
T.	Centaurium umbellatum		—	2	1·8										
H.s.	Cirsium acaule		—	1	1·5										
H.s.	Daucus carota		—	2	1·0										
H.s.	Ononis repens		—	1	1·0										
H.c.	Phleum pratense		—	2	1·5										
Ch.	Polygala vulgaris		—	1	2·0										
T.	Sisymbrium thalianum		—	1	1·0 l.										
T.	Trifolium arvense		—	1	1·3										
T.	T. procumbens		—	2	2·2										
Ch.	Veronica officinalis		—	1	1·0 l.										
T.	Arenaria tenuifolia	5	2·0	5	2·0	2	1·3								
H.s.	Astragalus danicus	1	1·0 l.	5	2·6	1	1·0								
T.	Crepis virens	3	1·1	4	1·8	1	1·5								
H.s.	Erigeron acre	2	1·8	1	1·3	1	1·0								
H.r.	Plantago lanceolata		+	1	1·0	1	1·0								
T.	Saxifraga tridactylites	5	1·9	5	1·8	1	2·0								
T.	Aira caryophyllea		—	5	2·3	4	1·4								
Ch.	Asperula cynanchica		—	4	3·2	1	2·3 l.								
G.r.	Carex ericetorum		—	4	2·1		+								
H.c.	Festuca rubra		—	1	2·0	1	1·0								
H.r.	Hypochaeris radicata		—	1	2·0	1	2·0								
H.s.	Lotus corniculatus		—	5	2·7	2	1·3								
T.	Sagina apetala		—	1	2·0	2	1·3								
H.s.	Sagina nodosa		—	4	2·0	1	1·7								
Ch.	Thymus serpyllum		—	5	4·1	2	1·8								
T.	Trifolium dubium		—	4	2·0	5	1·9								
Ch.	T. repens		—	3	2·5	4	2·1								
Ch.	Veronica chamaedrys		—	3	1·4	1	1·0								
T.	Vicia angustifolia		—	2	1·7	2	1·6								
H.c.	Anthoxanthum odoratum	1	1·0	3	2·5	3	2·0	1	2·0						
G.r.	Carex praecox	2	1·0 l.	5	2·7	5	3·1	3	1·7						
G.rad.	Cirsium arvense	5	2·0	2	1·6	5	1·9	3	1·9						
H.s.	C. lanceolatum	5	2·0	5	2·0	5	1·5	2	1·4						
T.	Draba verna	5	2·1	5	1·8	5	1·9	2	1·0						
Ch.	Sedum acre	5	1·9	5	2·5	5	1·6	3	1·2 l.						
H.r.	Taraxacum erythrospermum	5	2·0	5	2·1	5	2·8	4	1·8						
H.r.	T. officinale	5	2·0	5	1·9	5	1·9	2	1·0						
T.	Vicia lathyroides	2	1·4	2	1·8	4	1·9	1	2·0						
H.r.	Viola canina	3	1·4	1	1·0	3	1·7	4	2·5						
Ch.	Cerastium arvense		—	3	1·8	1	2·5	1	2·0 l.						
Ch.	C. triviale		—	5	2·6	5	2·0	2	1·0 l.						
T.	Ornithopus perpusillus		—	1	2·0	2	1·3	2	1·0						
Ch.	Sagina procumbens		—		—	2	1·4	2	1·0 l.						
T.	Arenaria serpyllifolia	5	2·0	5	1·9	5	2·0	3	1·0 l.	1	1·0 l.				
H.r.	Hieracium pilosella	5	1·9	5	2·2	5	1·6	2	1·0	1	1·0				

[1] C. = constancy. [2] A.F. = average frequency. [3] l. = local. [4] r. = rare.

	Grassland type …	A		B		C		D		E		F		G	
Life-form		C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.
T.	Hypochaeris glabra	4	2·0	3	1·7	3	2·0	5	2·0	2	1·0 l.				
H.c.	Koeleria gracilis	5	2·1	5	3·5	5	2·2	3	2·0	1	1·0 r.				
H.s.	Senecio jacobaea	5	2·0	5	2·2	5	2·8	5	2·2	2	1·5				
T.	Alchemilla arvensis	1	1·0 l.	4	1·4 l.	5	1·9 l.	5	1·7 l.	3	1·0 l.	2	1·0 l.		
H.s.	Campanula rotundifolia	1	1·0 l.	5	3·2	5	3·3	5	2·7	2	1·6	1	1·0		
T.	Cerastium semidecandrum	5	2·0	5	2·2	5	1·8 l.	4	1·3 l.	3	1·2 l.	2	1·0 l.		
T.	Myosotis collina	3	1·0 l.	5	2·0	5	2·4	5	1·6 l.	3	1·0 l.	2	1·0 l.		
T.	Veronica arvensis	4	1·5	5	2·0	5	2·2	5	1·0 l.	2	1·0 l.	2	1·0 l.		
H.c.	Agrostis canina A. tenuis	5	2·1	5	3·0	5	3·3	5	3·2	5	3·0 l.	5	3·0 l.	5	2·3l.
T.	Aira praecox	1	1·0 l.	5	2·4	5	2·1	5	2·0	5	2·5	5	2·5 l.	5	2·0l.
H.c.	Festuca ovina	5	4·1	5	4·0	5	4·4	5	4·0	5	2·8	5	2·6	5	2·8
H.s.	Galium verum	5	2·0	5	3·4	5	4·0	5	2·8	3	1·6	1	1·0 l.	1	1·0l.
H.r.	Luzula campestris	2	1·0	5	2·6	5	3·1	5	3·2	5	2·7	5	3·8	5	2·3
G.r.	Poa pratensis		—	2	1·2	1	1·0	1	1·5		—	1	1·0 l.		
T.	Sagina ciliata		—	2	1·5	5	2·0	4	1·0 l.	2	1·0 l.				
H.s.	Urtica dioica		—	1	1·0 l.	1	1·0 l.	5	1·0 l.	3	1·5 l.	2	1·0 l.		
H.s.-G.rad.	Rumex acetosella		—	5	1·9	5	2·8	5	3·5	5	2·2	5	2·8	5	2·1
T.	Teesdalia nudicaulis		—	1	1·5	5	1·6	5	2·8	5	2·3	5	1·0 l.	5	1·3 l.
Ch.	Galium saxatile		—		—	3	1·7	5	3·0	5	2·2	5	3·8	5	2·2

Bryophytes … …	A		B		C		D		E		F		G	
	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F
Barbula fallax		+												
Ditrichum flexicaule	5	2·9												
Thuidium abietinum	4	1·8	2	1·0										
Brachythecium purum		—	4	2·7										
Eurhynchium striatum		—	1	1·0										
Fissidens taxifolius		—	4	2·6										
Hypnum chrysophyllum		—	2	+										
Mnium rostratum		—	5	2·0										
Weisia microstoma		—	1	+										
Camptothecium lutescens	5	2·5	5	2·7	2	1·0								
Encalypta vulgaris	5	2·1	5	2·1	4	1·3								
Hylocomium rugosum	4	1·4	5	2·7	5	1·9								
Rhacomitrium canescens	2	1·0	1	1·5	1	1·0 l.								
Bryum roseum		—	3	2·0	4	2·3								
Eurhynchium megapolitanum		—	5	2·3	1	1·0								
Frullania tamarisci		—	4	2·3	3	1·8								
Hylocomium splendens		—	3	2·2	1	2·0								
H. squarrosum		—	1	2·0	1	2·0								
H. triquetrum		—	3	2·0	2	1·3								
Pottia lanceolata		—	1	+	2	1·0								
Tortula ruraliformis	2	1·0 l.	3	1·2 l.	2	1·0 l.	1	1·0 l.						
Climacium dendroides		—	1	1·0	1	1·5	1	1·0 l.						
Hypnum schreberi		—	3	2·0	5	2·7	3	2·2						
Lophocolea cuspidata		—	3	2·5	1	1·0	1	1·0						
Barbula rubella		—		—	1	1·0								
Cephaloziella hampeana		—		—	1	1·0								
Encalypta streptocarpa		—		—	1	1·0								
Pottia truncatula		—		—	1	1·0								
Scapania irrigua		—		—	1	1·0								
Webera nutans		—		—	2	1·0								
Bryum capillare	4	2·1	4	2·0	1	1·0		—		—	1	1·0 l.		
Hypnum cupressiforme	5	2·7	5	3·0	5	2·9	5	2·0	3	1·0 l.	3	1·0 l.	2	1·7
Brachythecium albicans		—	1	2·0 l.	2	1·5 l.	5	1·5 l.	2	1·0 l.	2	1·8 l.		
Lophozia barbata		—	3	2·3	5	2·1	5	2·3	3	1·3	1	2·0		
Cephaloziella starkii		—		+	3	1·7	4	1·1	5	1·6 l.	3	1·2 l.	4	1·3 l.
Ceratodon purpureus		—	4	1·9 l.	5	1·8 l.	5	3·0 l.	5	2·1 l.	5	2·7 l.	5	2·2 l.
Dicranum scoparium		—	5	3·3	5	3·3	5	3·7	5	2·6	5	2·8	5	3·0
Polytrichum juniperinum		—	1	1·3	5	2·5	5	2·2 l.	5	3·5 l.	5	3·0 l.	4	1·7 l.
Ptilidium ciliare		—	4	1·8	5	3·3	5	3·5	5	2·5	5	2·8	5	2·4
Lophozia excisa		—		—	5	1·6	5	1·9	2	1·3 l.	1	1·0 l.		
Polytrichum piliferum		—		—	1	1·0	4	2·0 l.	5	2·5 l.	2	2·3 l.	4	1·6 l.
Bryum sp.		—		—		—	4	1·5 l.	3	1·0 l.	1	+	1	1·0 l.

Lichens	A		B		C		D		E		F		G	
	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.	C.	A.F.
Lecanora lentigera	5	2·0												
Leptogium subtile L. turgidum	3	1·8												
Placodium fulgens	1	2·5												
Psora decipiens	5	2·8												
Biatorina coeruleonigricans	5	2·6		+										
Diploschistes scruposus	3	2·0	1	1·0										
Peltigera rufescens	5	2·0	5	2·0	1	1·5								
P. canina		—	2	2·0	5	2·0								
P. polydactyla		—	5	2·1	5	2·0	5	1·8						
Cladonia rangiformis	5	3·1	5	2·7	3	1·9	4	1·0 l.	2	1·0 l.	3	1·0 l.		
Cetraria aculeata	5	2·3	5	2·3	5	2·2	5	2·1	5	3·0	5	2·7	5	2·4
Cladonia alicornis	5	2·7	5	2·2	3	1·4	4	1·6	4	1·4	4	1·3	1	1·5
C. furcata	5	3·0	5	2·4	5	2·1	5	2·6	5	3·1	5	3·6	5	3·0
C. pyxidata	5	2·0	1	2·0	4	2·0	5	2·0	5	1·2	4	2·0	5	2·0
C. silvatica	3	1·3	5	3·3	5	4·3	5	4·5	5	5·0	5	5·0	5	5·0
C. uncialis	1	1·0		—		—	4	1·9	5	2·1	5	2·1	5	2·0
C. fimbriata		—		—	4	1·9	5	1·9	4	1·3	3	1·6	5	2·0
C. coccifera		—		—	3	1·7	2	1·0	3	1·3	2	1·5	3	1·5
C. pityrea		—		—	2	1·7	1	1·0	1	1·0	1	1·5	1	1·0
Biatora granulosa		—		—		—	1	1·0		—		—	2	1·3
B. uliginosa		—		—		—		—	5	1·0 l.	5	1·0 l.	5	2·0 l.
Cladonia bacillaris		—		—		—		—	2	1·0	2	1·0	3	1·9
C. floerkiana		—		—		—		—	1	1·0				

are, although rare, recorded from E only: *Campanula rotundifolia*, also very infrequent, grows in four plots in E, one only in F and is absent from G; *Urtica dioica* has a similar distribution while *Galium verum* has a constancy of 3 in E, is local in one plot in F and finds a place in G because of the record of two plants only. Incidentally, *Juncus squarosus* is a very rare plant in G, although not recorded from any plot.

Again in the disturbed soil of the nettle patches and in soil thrown up from rabbit burrows the same differentiation is suggested. *Arenaria serpyllifolia*, *Sagina ciliata* and *Stellaria media* are confined to E: *Alchemilla arvensis*, *Cerastium semidecandrum*, *Myosotis collina*. *Veronica arvensis*, *Brachythecium albicans* and *Cladonia rangiformis* to E and F while *C. alcicornis* has a constancy of 4 in E and F and 1 only in G.

In all these variants the removal of the lichen carpet where it is unmixed with vascular plants discloses the easily identifiable remains of *Agrostis*, *Festuca*, *Rumex*, *Luzula*, *Galium* and occasional pieces of *Calluna*. It is thus clear that these species once grew there. General observations over a period of years supplemented by careful records from 1936 to 1938 (inclusive) show the marked fluctuations in number which take place. Thus, as already mentioned, E was red with flowering *Rumex* in 1933 and nothing comparable has been seen since: and in the plots for careful record the percentage of small squares in which *Rumex* occurred was 0·7, 11·8 and 0·4 respectively for 1936, 1937 and 1938. Similar fluctuations are recorded for *Agrostis* and *Galium*, both inside and outside the rabbit-proof enclosures. These variations in number do not run parallel for the different species: for the same years the percentages for *Agrostis* outside the enclosure are roughly 7, 28 and 54 and for *Galium* 49, 26 and 10. The subject is not further elaborated here, but the hypothesis of a cycle of change bound up with climate and plant competition is being investigated. If this hypothesis is sound the greater abundance of *Luzula* and *Galium* in F may be a temporary manifestation of a particular phase in the cycle.

Death of the higher plants leaves the lichen carpet anchored by their dead remains. On decay disintegration follows and bare soil is exposed (Pl. 5, phot. 5) but the process of decay is slow and disruption is long delayed or may not even take place before reinvasion by higher plants restabilizes the carpet. At present in E and F disintegration is local. But in G about 50% of the area is thus denuded. The slight erosion which follows is checked by recolonization by higher plants, very slowly by *Agrostis* spp. vegetatively from marginal relics, by *Aira praecox*, *Festuca ovina*, *Rumex acetosella* and *Teesdalia nudicaulis* by seed. Of these *Aira* is numerically the strongest but *Festuca* is the most important as it is perennial. The higher plants provide anchorage for lichens and the course of development of the vegetation on the denuded patches follows the lines already described (Watt, 1938). In this way is explained the occurrence of occasional patches of abundant tufted fescue set in a background of lichen—a phenomenon unintelligible unless explained in terms of development.

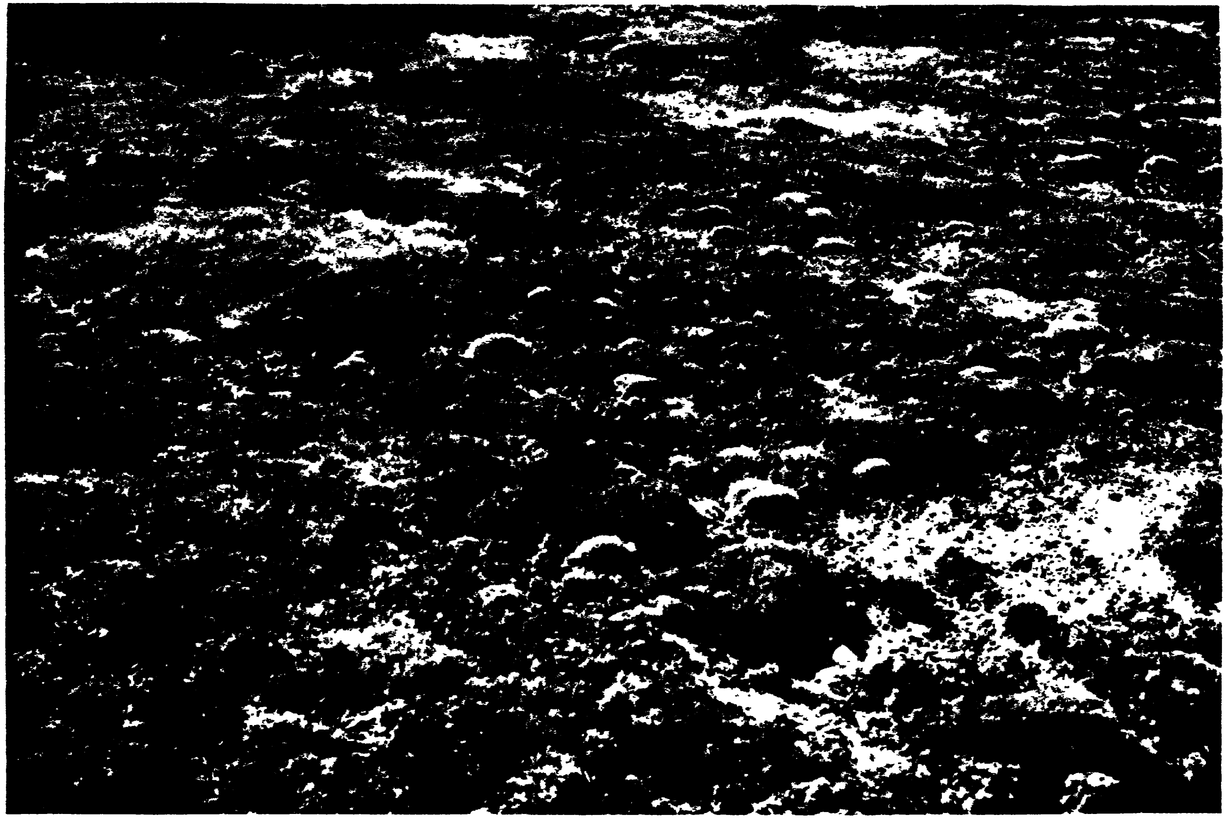
SUMMARY

The so-called "grass-heath" of Breckland shows much variation in its floristic composition and physiognomy.

This variation is causally related primarily to the soil and secondarily to other factors (e.g. grazing by rabbits) still under investigation.

The soil is derived from the chalky boulder clay which by progressive decalcification and podsolization shows a series of stages in soil profile development from highly calcareous shallow immature soils to a deep well-marked podsol. Seven stages are recognized and the profile in each described and figured. From each horizon (or at successive depths in the profile) data of the acidity and the content in calcium carbonate, carbon and sesquioxides are graphically presented. From composite surface (0–15 cm.) samples from each type data have been obtained (and tabulated) of the exchangeable calcium, total exchangeable bases, acidity, carbon and nitrogen contents. Tests of acidity on composite surface (0–4 cm.) samples from each plot in each type have been made and the data graphed.

The data show that we are dealing with a series in the genesis of a podsol: the increase in soil depth and in acidity, the decrease in calcium carbonate and in base status as well as in the change in the kind of humus from mull to mor and the movement of the sesquioxides confirm this interpretation. The acidity of the surface (0–4 cm.) samples suggest two levels of relative stability separated by a stage of rapid change. The moisture relations in this series of profiles must also vary but no determinations have been made.



Phot. A. Burges

Phot. 5. Grassland G. The vegetation is patchy: the *Cladonia* mat in different stages of disintegration exposes some bare soil. Rounded hummocks are grazed tussocks of fescue; the lighter patches at the top of the picture are *Agrostis* spp.

The first five stages in the series are separated by significant differences in the quantitative estimates of the factors: the last two are essentially the same as the fifth.

On the basis of their ecological requirements the species are classed into four groups, calcicole, exacting, calcifuge and tolerant. When arranged in arrays the serial change in the flora from soil stage to soil stage is at once obvious: the calcicoles are confined to the first two stages which contain calcium carbonate and are alkaline, the exacting species have a wider range generally covering the first four: the calcifuges make their appearance in the third stage when the soil becomes acid and the tolerants are indifferent being found in all stages.

This primary differentiating basis when considered in relation to the total flora of vascular plants and bryophytes brings out the significant fact that the drift in the number of species from the second stage to the last is due mainly to the progressive elimination of species and not to a radical change in the flora. (The lichen flora on the other hand shows greater specific variation.) The scarcity of calcifuges on the acid soils is probably due to grazing by rabbits and the dryness of the habitat, and dryness is also probably the primary cause differentiating the communities on the first and the second soil stages.

The flora is drought resistant or drought evading: there are very few broad-leaved herbs. Physiognomically the outstanding feature is the high percentage of annuals and the increase in the sociability of *Cladonia silvatica* from the third stage: in the last three stages *C. silvatica* is the dominant plant.

Using narrow ecological requirements and high constancy and high abundance as sifting criteria we find that the first five communities, corresponding to the first five stages in profile development, are significantly different from each other. Vegetationally the last three are essentially the same. They differ however in minor features which suggest the possibility of there being different phases in a cycle of change, causally related to the development of the lichen carpet and to the periodic climatic changes in a region with a climate transitional between oceanic and continental.

The vegetation on each soil type is described and characterized.

The data given in the paper afford convincing proof that soil is a primary differentiating factor in the "grass-heath" of Breckland.

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THE ROLE OF BRYOPHYTES IN THE CALCAREOUS FENS OF THE OXFORD DISTRICT

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INTRODUCTION

THE fens of the Oxford district fall into two main categories: those in which deep valley-basins, supplied with water by small streams and by seepage from the sides, have accumulated a considerable thickness of calcareous peat; and those on hillsides where seepage water flows through pervious sandy strata above a substratum of clay, and where peat is scanty. In both types the water entering the area is derived from Corallian beds and is highly calcareous, and the water table is maintained at a high level; and in both *Juncus obtusiflorus* is always an important constituent of the vegetation. They differ in that water can collect and stagnate in the deeper peat-filled basins, except in the neighbourhood of the natural or artificial streams which flow through them, and which are usually too shallow to act as efficient drains. The hillside fens, on the other hand, are better flushed by virtue of their slope, but are permanently wet because water seeps continually through them from the junction of pervious with impervious strata. The significance of this difference lies, presumably, in a higher oxygen and nitrate content in the better flushed habitats. The vegetational differences arise in part, however, from the fact that there has been peat cutting in the past in almost all of the fens of the basin type. The effect of this is to increase very considerably their range in water level, since water collects in the deeper cuttings and brings about partial drainage of the surrounding higher ground. Peat cutting has also initiated successions of plant communities with a large range in the depth of water at their starting-points. The water is, however, never very deep, and the longest successions are short compared with those to be seen in the Norfolk Broads, the English Lakes or the Shropshire Meres; and some must have begun with water close to the peat surface.

The earliest phanerogamic colonizer of standing water over 6 in. deep is *Phragmites*, and this is followed by *Juncus obtusiflorus*, which initiates the succession when *Phragmites* is absent. The Juncetum may be followed by a community in which *Schoenus nigricans* shares dominance with *Juncus obtusiflorus*, with *Carex paniculata* as a frequent associate. Where no biotic factors prevent the establishment of woody plants, *Salix cinerea*, *Alnus rotundifolia* and *Betula pubescens* colonize the *Juncus* or *Juncus-Schoenus* community, forming first an open willow-alder carr and later a closed alder carr in which *Carex paniculata* tussocks are prominent at first, *Juncus* and

Schoenus soon disappearing as the result of shading. The alder carr is succeeded by ash or birch woods on more or less calcareous peat respectively, and there is some evidence that the succession culminates in an oak wood on peat.

When the peat cutting is shallower, so that there is little standing water, the succession differs in the earlier appearance of *Schoenus* with consequent shortening of the *Juncus* stage; and in the insignificant part played by *Carex paniculata*, which luxuriates only in fairly deep water.

When there is no permanently standing water above a cut and compacted peat surface, *Juncus* and *Schoenus* colonize with difficulty. The first plant community is very mixed, the chief species being a number of small sedges (*Carex flava*, *panicea*, *dioica*, *pulicaris*, etc.), *Eriophorum latifolium* and *E. angustifolium*, *Pedicularis palustris*, *Parnassia palustris*, *Valeriana dioica*, *Drosera rotundifolia*, *Pinguicula vulgaris*, *Anagallis tenella* and marsh orchids. Shrubs and trees may invade this directly.

The successions outlined above can rarely be seen as complete zonations in any one area, since there is usually deflexion by drainage or by cutting, burning and grazing, preventing the establishment of woody plants. Under these circumstances various herbaceous communities arise whose floristic composition depends on the average height and seasonal change of the water table, the frequency of burning and cutting and the intensity of grazing. The *Schoenus* stage is much prolonged and is succeeded by communities dominated by *Molinia*, *Filipendula*, *Arrhenatherum* and *Brachypodium pinnatum*. With cessation of burning, cutting and grazing woody plants can invade any of these communities.

THE ROLE OF BRYOPHYTES IN COMMUNITIES OF THE PRIMARY SUCCESSION

(1) Phragmites *and* Juncus *stages*

No bryophytes occur amongst *Phragmites* and *Juncus* in water more than 3 or 4 in. deep. When the shade cast by *Phragmites* and *Juncus* is not too great the first moss to appear is *Campylium* (*Hypnum*) *stellatum* which establishes itself on their shoots at water level and soon spreads to form large mats. These project slightly above average water level, and are at first floating, supported by the shoots of the phanerogams. Their under sides become heavily calcified, and they contribute largely, with *Chara*, to the calcareous peat formed in this stage of the succession. Occasionally shoots on which *Campylium* has established itself break off and fall to the bottom of water a few inches deep and give rise to submerged mats. The moss differs somewhat in form under these conditions, its shoots being prostrate with pinnate branching and with leaves less squarrose than usual, and it becomes heavily encrusted with calcium carbonate.

Whether they begin floating or submerged, the mats ultimately reach from the calcareous floor to average water level, and neighbouring mats merge to form extensive continuous carpets. Features of this stage are the occurrence of *Aneura pinguis*, especially in its slender form *angustior* Hook.; and of *Campylium* (*Hypnum*) *helodes*, whose slender pinnate shoots climb 2-5 in. up the shoots of phanerogams, sometimes completely encircling them, and often fruiting freely just above water level.

When the water becomes somewhat shallower other mosses appear, first *Calliergonella* (*Hypnum*) *cuspidata*, then *Drepanocladus* (*Hypnum*) *revolvens*, *D. intermedium*, *Cratoneurum glaucum* (*Hypnum commutatum*), *C.* (*Amblystegium*) *filicinum* and *Mnium Seligeri*, all mat-forming species. These may establish themselves in the same way as *Campylium stellatum* or may invade mats of this moss.

Where *Phragmites* is sufficiently dense to cast a deep shade, or a pure Juncetum is especially luxuriant, *Campylium stellatum* is rare or absent, apparently because intolerant of shade. Its place is taken by *Calliergonella cuspidata* which establishes itself in a similar way, and from which slender ascending branches climb shoots of *Phragmites* and *Juncus* in much the same way as *Campylium helodes* in less shaded situations.

These extensive moss mats are important in consolidating the loose calcareous surface, and in forming a starting-point for the seedlings of many phanerogam species such as *Schoenus nigricans*, *Valeriana dioica*, *Pedicularis palustris*, *Cardamine pratensis*, *Orchis praetermissa*, *Oenanthe Lachenalii*, *Betula alba*, *Salix cinerea*, *Alnus rotundifolia*, *Fraxinus excelsior*, *Pinus sylvestris*, etc. Their suitability for this purpose arises from their being permanently moist at the surface, but not submerged except after heavy rain. Since the mats are first formed where shoots of *Juncus* and *Phragmites* are most dense, little colonies, including several different species of phanerogams, arise in such places and constitute areas where peat formation and raising of the surface above water level are most rapid. Pioneer shrub and tree seedlings are very frequently established in this way.

(2) *Dwarf sedge stage on wet compacted peat*

The dwarf sedge community on cut peat which has a very high water table but is not often submerged, is characterized by a great luxuriance and richness of the bryophyte flora. Mosses form an almost continuous carpet upon which phanerogamic seedlings establish themselves. The carpet is a mosaic of patches of several different species of mosses of which *Drepanocladus revolvens*, *Campylium stellatum*, *Calliergonella cuspidata*, *Cratoneurum filicinum*, *C. glaucum*, *Philonotis fontana*, *Mnium affine*, *Mn. Seligeri*, *Mn. punctatum* and *Bryum ventricosum* (*pseudotriquetrum*) are the most important. As establishment of phanerogams proceeds the area occupied by mosses becomes restricted, and shade-tolerant species such as *Calliergonella cuspidata* and *Mnium* spp. constitute an increasing proportion of the moss carpet.

(3) Juncus-Schoenus *stage*

With the entry of *Schoenus*, drier habitats for bryophytes are afforded by the tops and sides of its tussocks. The youngest tussocks have *Campylium stellatum* or *Calliergonella cuspidata* covering even their tops but on somewhat older tussocks *Fissidens adiantoides* and *Ctenidium* (*Hypnum*) *molluscum* appear at the top, while the low ground between tussocks is still too wet for them. On still older tussocks there is a zonation with *Campylium*, *Calliergonella*, *Drepanocladus* spp. and *Aneura pinguis* at the base, *Fissidens adiantoides*, *Bryum ventricosum*, *Mnium* spp. and *Aneura multifida* on the sides and *Ctenidium molluscum*, *Campylium* (*Hypnum*) *protensum* and *Pseudoscleropodium* (*Brachythecium*) *purum* on the top (cp. Watson, 1932). Tussocks of *Carex paniculata* show a comparable zonation but, because of their greater height, species tolerant of still drier conditions, such as *Oxyrrhynchium* (*Eurhynchium*) *praelongum*, *Brachythecium rutabulum* and *Lophocolea bidentata* may form a zone above *Ctenidium* and *Pseudoscleropodium*. The mosses continue to form a favourable substratum for the germination and establishment of various species of phanerogams, and also permit the entry of acidiphilous species both of bryophytes and phanerogams (see below, p. 77).

(4) *Wet carr stages*

In wet carr *Campylium stellatum* is no longer found, apparently being intolerant of shade. The dominant moss in wetter places is *Calliergonella cuspidata* with *Brachythecium rutabulum*, *Mnium undulatum*, *Mn. punctatum* and *Mn. affine*, all frequent on mud and at the margins of pools. Special habitats are afforded by the sides and tops of *Carex paniculata* tussocks and by the bases and dead stumps of woody plants. In early stages of carr when the shade is not very heavy the tussocks of *Carex* are tall and healthy and show a well-marked zonation of bryophytes. *Calliergonella* and *Mnium* spp. occur on the mud at their base; *Mnium undulatum*, *Brachythecium rutabulum*, *Oxyrrhynchium praelongum* and *Lophocolea bidentata* on their sides; and *Oxyrrhynchium*, *Pseudoscleropodium*, *Brachythecium*, *Thuidium* and *Lophocolea* on their tops. As the shade in the carr becomes deeper the *Carex* tussocks degenerate and soon become flat-topped stumps with only a few living shoots persisting. In the early stages of this degeneration the epiphytic moss flora attains its maximum luxuriance and most clearly defined zonation. As degeneration proceeds the decomposing shoots and adventitious roots become strongly acid in reaction, and a number of acidiphilous mosses appear. Thus the following species were observed on moribund and dead tussocks in carr at Headington Wick: *Mnium hornum* (abundant), *Polytrichum formosum*, *Tetraphis pellucida*, *Campylopus fragilis*. During later stages of retrogression the bryophyte zonation becomes less marked, tussocks being found with *Mnium* spp. above and *Calliergonella* below, and, finally, dead stumps projecting only an inch or two above fetid black mud are completely covered with *Calliergonella* on which many phanerogam seedlings (*Filipendula Ulmaria*, *Valeriana dioica* and *V. sambucifolia*, *Scabiosa succisa*, *Cirsium palustre*, etc.) establish themselves.

Mnium undulatum, *Mn. punctatum*, *Mn. affine*, *Calliergonella cuspidata*, *Oxyrrhynchium praelongum*, *Calypogeia fissa*, *Lophocolea bidentata*, *Plagiochila asplenioides* and *Aneura multifida* are the most frequent bryophytes on and round the bases of woody plants. There are also found here, especially on old stools and dead stumps of alder, a number of acidiphilous species, chief among which are *Mnium hornum*, *Pellia epiphylla* and *Sphagnum plumulosum*. Their occurrence in a highly calcareous carr appears to depend on the relatively high acidity of alder bark, though extensive patches of *Sphagnum* may persist from an earlier *Phragmites-Juncus* stage in which they are initiated on mats of other species of moss (see below, p. 77). With increasing shade and heavier litter *Sphagnum* soon becomes unhealthy, and it plays no important part in mature carr.

COMMUNITIES OF THE DEFLECTED SUCCESSIONS

(1) *Late Juncetum*

Schoenus nigricans is not an invariable feature of the fen succession and in its absence *Juncus obtusiflorus* retains dominance to a later stage. If woody plants are allowed to come in, the *Juncus* is gradually shaded out, persisting in the non-flowering condition when the shade is light and disappearing altogether under a closed canopy of alder. When woody plants are excluded, as when the rushes are cut for litter, *Juncus* persists much longer and may still be found in the dry community dominated by *Brachypodium pinnatum*. When competition with *Schoenus* and shading by woody plants set no check to its growth the *Juncus* forms a luxuriant and often almost pure community, reaching about a metre in height. Its growth is optimal in 1–3 in. of standing water when it casts too much shade for successful growth of *Campylium stellatum* and by far the most abundant moss is *Calliergonella cuspidata* which forms extensive mats and provides a nidus for the establishment of phanerogamic seedlings. *Mnium* spp., *Fissidens adiantoides* and *Bryum ventricosum* are occasional associates.

(2) *Molinio-Juncetum*

The next stage in a succession with *Schoenus* absent and woody plants excluded by cutting or burning is characterized by the increasing abundance of *Molinia coerulea*, which first attains codominance with and later dominance over the *Juncus*. It enters the Juncetum on moss mats and soon forms little tussocks which increase in size and frequency as the accumulation of peat lowers the water table. These *Molinia* tussocks show a bryophytic zonation similar to that on *Schoenus* and *Carex paniculata*. Thus the smallest tussocks are covered with *Calliergonella cuspidata* while rather older tussocks show *Calliergonella* at the base, *Fissidens adiantoides* and *Ctenidium molluscum* on the sides, with *Pseudoscleropodium purum*, *Campylium protensum*, *Mnium affine* and *Calypogeia fissa* at the top.

(3) *Late Schoenetum*

When the establishment of woody plants is arrested by frequent fires *Schoenus*, which cannot persist in the shade of the carr, maintains itself as a dominant up to a stage where there is no longer any standing water between the tussocks. Towards the end of this period, the tops of the tussocks become colonized by *Molinia*, *Brachypodium pinnatum* and many other species and the *Schoenus* is gradually killed as a combined result of competition and desiccation. Fires, by removing dead leaves and flowering stems, keep the sides of the tussocks and the channels between them free from litter and enable bryophytes to flourish (Dawkins, 1939). Where shallow water persists between the tussocks *Calliergonella cuspidata*, *Campylium stellatum*, *Drepanocladus revolvens*, *D. intermedium*, *Amblystegium serpens*, *Ctenidium molluscum* are found between the tussocks; while *Fissidens adiantoides*, *Ctenidium molluscum*, *Bryum ventricosum*, *Campylium protensum* and *Calypogeia fissa* occur on the sides, and *Calypogeia fissa*, *Pseudoscleropodium purum* and *Ctenidium molluscum* on the tops of the tussocks. If there is no or very little water the first five of these become rare or absent and *Ctenidium* dominates the lows. Occasionally tussocks bear patches of *Sphagnum plumulosum* and *Aulacomnium palustre*.

(4) *Molinietum*

When *Molinia coerulea* becomes dominant its large tussocks are separated by low ground covered by dense *Molinia* litter except where this is removed by cutting or burning. Conditions are very unfavourable for growth of bryophytes and there is only scanty etiolated *Calliergonella cuspidata* and *Brachythecium rutabulum*. *Pseudoscleropodium purum* and *Calypogeia fissa* occur sparsely on the tussocks, the latter abundant on recently burned tussocks.

(5) *Drier communities*

Communities with *Filipendula*, *Arrhenatherum*, *Calamagrostis epigeios*, and *Brachypodium pinnatum* as dominants or important constituents differ from the communities already described in being drier and in having a more complete surface covering of flowering plants. Bryophytes are rare except in moister patches. *Brachythecium rutabulum*, *Pseudoscleropodium purum* and *Calliergonella cuspidata* occur very sparsely and are ecologically unimportant.

SUMMARY OF ZONATIONS

The results of the two preceding sections can be conveniently summarized in the form of a table showing the relation of the various species of mosses and liverworts to the average water level. Species confined or nearly confined to shade are given in brackets.

In shallow water	*Campylium stellatum, Calliergonella cuspidata, Aneura pinguis*
On peat with water at or close to the surface	*Campylium stellatum, Calliergonella cuspidata, Drepanocladus revolvens, D. intermedium, Mnium Seligeri, Mn. punctatum, Mn. subglobosum,* [*Mn. undulatum*], *Philonotis fontana, Cratoneurum glaucum, Cr. filicinum*
Just above water level, at base of tussocks, etc.	*Aneura multifida, Fissidens adiantoides, Bryum ventricosum, Sphagnum plumulosum, Aulacomnium palustre, Campylium helodes*
Sides of tussocks, etc.	*Ctenidium molluscum, Mnium affine*
Tops of tussocks, etc.	*Pseudoscleropodium purum, Calypogeia fissa, Campylium protensum, Hypnum cupressiforme, Brachythecium rutabulum*
Tops of high tussocks, etc.	*Oxyrrhynchium praelongum, Lophocolea bidentata,* [*Thuidium tamariscinum, Mnium hornum, Pellia epiphylla*]

THE OCCURRENCE OF *SPHAGNA* IN THE FEN SUCCESSION

Sphagnum plumulosum is locally abundant in two of the fens near Oxford, at Cothill and at Marcham Bog, and was recorded by Sibthorp (1794) for Bullingdon Bog, but is no longer to be found there. Since the water and peat of all these fens is highly calcareous it becomes a point of interest to investigate the conditions under which *Sphagnum* is able to establish itself and spread in these localities.

In Marcham Bog and in one of the peat cuttings at Cothill *Sphagnum plumulosum* occurs in patches 1–18 ft. in diameter in the late *Phragmites-Juncus* stage when woody plants are colonizing actively. These patches or hummocks are hollow so that the *Sphagnum* is not directly in contact with the peat surface but is supported by the bases of shoots of *Phragmites* and *Juncus*. At its periphery the patch advances over a mat of other mosses of which *Mnium Seligeri*, *Mn. punctatum*, *Mn. subglobosum*. *Mn. undulatum*, *Calliergonella cuspidata*, *Bryum ventricosum* and *Campylium stellatum* are the most frequent. In one place three shoots of *Sphagnum* were found isolated in a luxuriant mat of *Calliergonella* with a little *Mnium Seligeri*, and there seems no doubt that *Sphagnum* normally establishes itself and spreads amongst other mosses.

In another of the peat cuttings at Cothill patches of *Sphagnum* of all sizes are colonizing the sides and tops of *Schoenus* tussocks. At first it was thought that this must be consequent upon an increased acidity of the peat surface when raised above water level, but *p*H determinations did not support this explanation. Three tussocks yielded the following results:

	Depth below surface in cm.	*p*H
(1) An old tussock bearing *Molinia coerulea, Festuca rubra, Potentilla erecta, Scabiosa succisa, Valeriana dioica, Calypogeia fissa*	9– 4	7·5
	4– 8	7·4
	8–12	7·5
(2) Older tussock with *Molinia, Brachypodium, Parnassia, Polygala, Valeriana dioica*, etc., and *Calypogeia fissa, Pseudoscleropodium purum, Mnium punctatum* and *Ctenidium molluscum*	0– 5	7·5
	5–10	7·5
	10–15	7·5
(3) Still older tussocks with living shoots of *Schoenus* confined to the sides and *Festuca rubra* dominant on top surrounded by a ring of *Molinia. Calypogeia fissa, Campylium protensum* and *Fissidens adiantoides* in the *Molinia* ring	0– 6	7·3
	6–12	7·5
	12–18	7·5
	18–25	7·5

Close examination showed that here, too, *Sphagnum* is invading a mat of other mosses and is not colonizing the bare peat of the tussock. Determinations were therefore made of the *p*H of water squeezed from the moss covering of *Schoenus* tussocks of progressively increasing age:

	*p*H
(1) *Campylium stellatum* from youngest *Schoenus* tussocks, under water on the day of sampling	7·4
(2) *Campylium* with a little *Calliergonella cuspidata* just above water level	7·4
(3) *Campylium* with black humified remains beneath	7·3
(4) *Campylium* on a tussock bearing three small shoots of *Molinia* with *Parnassia, Eupatorium, Drosera, Scabiosa succisa* and seedlings of *Angelica*	6·5
(5) *Ctenidium molluscum* with some *Campylium* and *Fissidens adiantoides* on an old tussock bearing *Molinia, Phragmites, Parnassia, Drosera, Scabiosa succisa* and a seedling of *Pinus sylvestris*	6·3

Acidity determinations were also made on water squeezed from the moss mat over which *Sphagnum* is advancing, and of the surface peat beneath the moss at Marcham Bog:

	*p*H
(6) Water from mat of *Mnium subglobosum*	6·9
Surface peat beneath mat	7·9
(7) Water from mat of *Mnium* spp. and *Bryum ventricosum*	5·5
Surface peat beneath mat	8·0

Lastly, water was squeezed from a moss mat bearing *Drosera rotundifolia* at Cothill:

	*p*H
(8) Water from mat of *Ctenidium molluscum, Drepanocladus revolvens* and *Campylium stellatum*	5·8

It would appear, therefore, that *Sphagnum plumulosum* (and *Aulacomnium palustre*, which occasionally occurs with it) is able to grow in a habitat with highly calcareous ground-water and peat because it establishes itself on moss mats the water in contact with which is made acid by selective ionic absorption. Small patches of *Sphagnum* are also found round the bases of pioneer alders and the stumps of burned pines, birches and willows in the *Juncus-Schoenus* stage, and on dead alder stumps in the closed carr at Cothill. Alder stumps also bear *Mnium hornum* and *Pellia epiphylla*, and it was inferred that they must be much more acid than the surrounding peat. This was confirmed by *p*H determinations of surface debris from an alder stump bearing a small patch of *Sphagnum*:

	*p*H
(1) From beneath the patch of *Sphagnum*	5·4
(2) Not beneath *Sphagnum*, but from a stump on which *Sphagnum* grew elsewhere	4·9

These figures show clearly that alder stumps provide a favourable habitat for *Sphagna*.

These investigations on the mode of establishment of *Sphagnum* are of especial interest in view of work on the entry of acidiphilous species into the fen succession at Calthorpe Broad, Norfolk (Godwin & Turner, 1933). Here it was shown that various *Sphagna* including *S. plumulosum* are locally abundant especially in young birch carr and in mowing meadows dominated by *Phragmites*, *Juncus obtusiflorus*, and *Carex* spp. These, it is pointed out, are all habitats which give some shading with consequent protection from desiccation but not the dense shade which normally excludes *Sphagna*. Numerous determinations show that when the fen peat is sufficiently above the reach of flood water it becomes steadily more acid in reaction until the surface soil in a mixed wood of oak, pine, ash and alder has a *p*H as low as 4·6. They ascribe the entry of *Sphagna* to this increasing acidity of the peat which they regard as a normal result of vegetational succession in this originally alkaline Broad. Conditions in the basin fens of the Oxford district are different in that the peat is so highly calcareous that it does not readily become acid on lowering of the water table, as the figures quoted above make clear. Acidiphilous species such as *Sphagnum plumulosum*, *Aulacomnium palustre*, *Mnium hornum*, *Pellia epiphylla*, *Drosera rotundifolia* and *Eriophorum angustifolium* are nevertheless present because the mats of fen mosses and the bases of woody plants provide substrata comparable in acidity with the surface peats of the Broads district. As at Calthorpe Broad *Sphagna* are prominent only in a short middle phase of a succession, with little or no standing water and with *Phragmites*, *Juncus* and scattered woody plants providing a light shade. In the closed carr stage the *Sphagna* are shaded out.

SUMMARY

Bryophytes play an important part in the succession from open water to carr in the highly calcareous fens of the Oxford district. *Campylium* (*Hypnum*) *stellatum*, and *Calliergonella* (*Hypnum*) *cuspidata* are the most abundant mosses in earlier stages, forming extensive mats upon which phanerogamic seedlings establish themselves. These mosses contribute very largely to the calcareous peat formed at this stage.

In later stages many other species appear and show characteristic zonations on tussocks of *Schoenus*, *Carex paniculata* and *Molinia*.

Sphagnum plumulosum cannot colonize the calcareous peat directly, but can establish itself upon and spread over mats of other mosses. It is shown that although the ground water is highly calcareous water squeezed from these mats has an acid reaction. Acidiphilous species are also found on alder stumps and on old tussocks of *Carex paniculata.*

Sphagnum plumulosum is prominent only for a short period, being tolerant neither of exposure nor of the shade of closed carr.

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VEGETATION OF A CALCAREOUS INNER FJORD REGION IN SPITSBERGEN

By A. M. ACOCK

(*With Plates 6 and 7 and three Figures in the Text*)

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I. INTRODUCTION

PLANT ecological studies in the Arctic have in the main aimed at the provision of the broad descriptive basis necessary as a preliminary to more intensive investigation. Such a general foundation has been laid in the case of Spitsbergen by a number of workers (Summerhayes & Elton, 1923. 1928; Michelmore, 1934; Scholänder, 1934). Here, therefore, an attempt has been made to provide a sufficiently detailed picture of vegetation and its environment in a restricted area to permit of comparison with other localities. and some analysis of environmental influences differentiating communities.

Summerhayes & Elton (1923, p. 258), Walton (1922) and Dobbs (1939) have provided a background of general information about the area described here, which is a strip of country near Bruce City, Klaas Billen Bay (see Fig. 1, shaded oblong). It has the additional advantages of possessing a number of distinct vegetation types and of being directly adjacent to the scene of the detailed work of Walton and Dobbs in such a way that some of the communities described here are later stages in the development of earlier seral stages dealt with by these workers. Further, the vegetation is typical of a fairly extensive calcareous inner fjord region (Summerhayes & Elton, 1928).

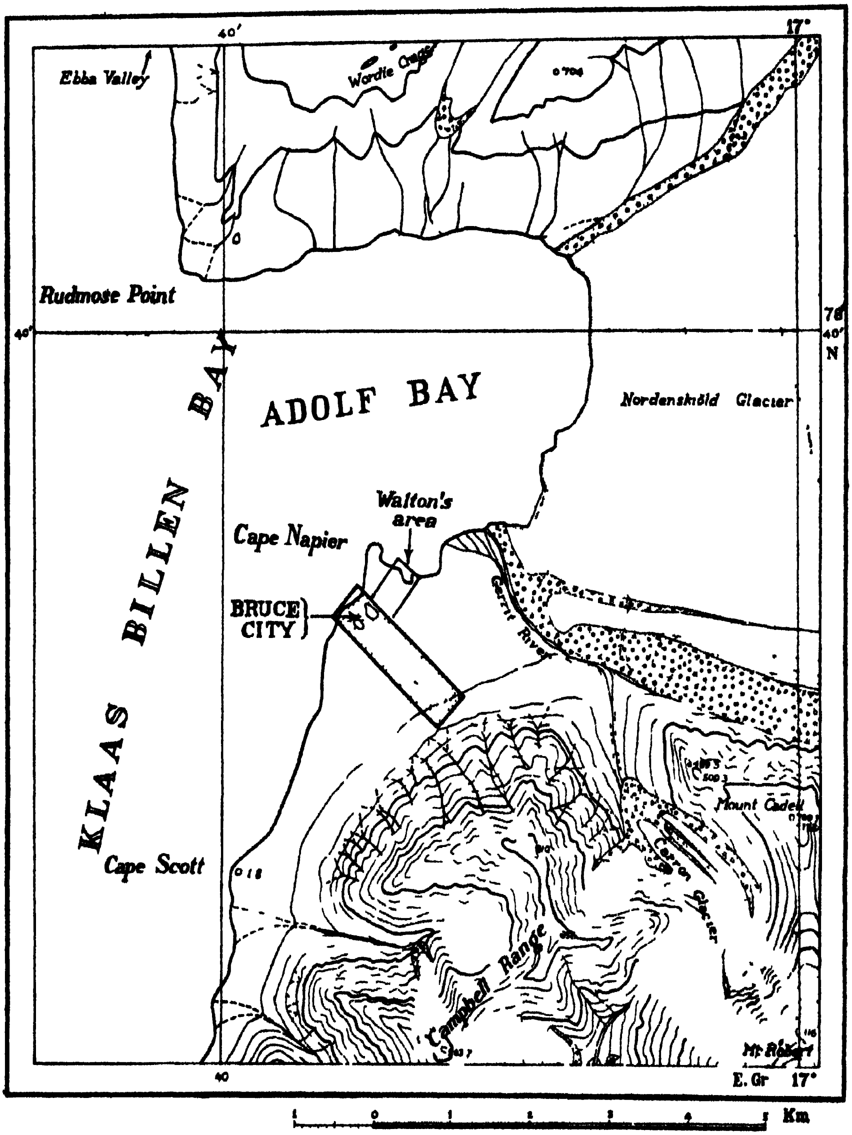

Fig. 1. Adapted from the boundary map of the area belonging to the Svenska Stenkolsaktiebolaget Spetsbergen produced by Det Norske Svalbardekspedisjonane, 1924, led by Adolf Hoel. 50 m. contour interval.

Description of the site

Climatic conditions. The eco-climate of Klaas Billen Bay shares, of course, the general features of high Arctic regions in respect of light and dark alternation, winter severity, permanently frozen subsoil and wet conditions accompanying snow-melting in spring (cf. Elton, 1927).

Local weather conditions most worthy of record seem to be:

(i) Comparatively warm summer conditions with air temperatures of 4–12° C., absence of frost and of permanent snow patches at low altitudes. 5 cm. soil temperatures as high as 20° C. were recorded.

(ii) Absence of fog and moderate cloudiness (*c.* $\frac{4}{10}$ in. in July-August 1936).

(iii) Low summer precipitation resulting in general aridity. Total annual precipitation is also very low.

(iv) Prevailing cold winds from the Nordenskjöld Glacier and New Friesland Ice Cap, and frequent southerly winds. Summer wind velocities are not high (usually not exceeding 15 m./sec., i.e. 22 m.p.h.).

The water relations of the region seem to agree substantially with those outlined for Reindeer Peninsula (Summerhayes & Elton, 1928). The soil, very wet after snow melting, dries out owing to rapid evaporation and drainage resulting from the porous nature of much of the soil, prolonged insolation and frequent winds. Water supply is mainly from snow water, streams, pools and melting ground ice.

Topographical features and habitat types. A survey (Fig. 2*a*), for which I am indebted to Mr T. W. J. Taylor, has been included of the sample strip of country to illustrate topographical features. Heights are referred to an arbitrary level, roughly corresponding to high water mark ordinary tides. Contours are at 5 ft. (1·52 m.) intervals, but after 75 ft. (22·9 m.) where the angle of slope is considerable, 25 ft. (7·6 m.) form lines are resorted to. Beach escarpments are marked in addition to contours. The area studied is a strip 570 yards (521 m.) in width running from the sea in a south-easterly direction towards the Campbell Range. It includes at the seaward end a system of raised shingle beaches in which eight main steps are recognizable. These have been numbered commencing with the lowest; raised beach 2 (RB 2), which is outside the area, is a gentle slope from Cape Napier to the flat on which pool VI is enclosed (RB 3). There is a series of pools and small moss bogs apparently arisen by enclosure of swampy mud flats behind shingle spits (cf. Walton), the whole subsequently elevated by a general raising of the land level in relation to the sea. Pools are numbered according to Summerhayes & Elton (1923), and bogs according to the pools with which they are associated. The wide upper beach (RB 8) is traversed by a number of snow-water streams and is heavily silted. At the foot of the mountain range, which rises quite abruptly from the silted beach plateau, there is a swampy silted zone kept

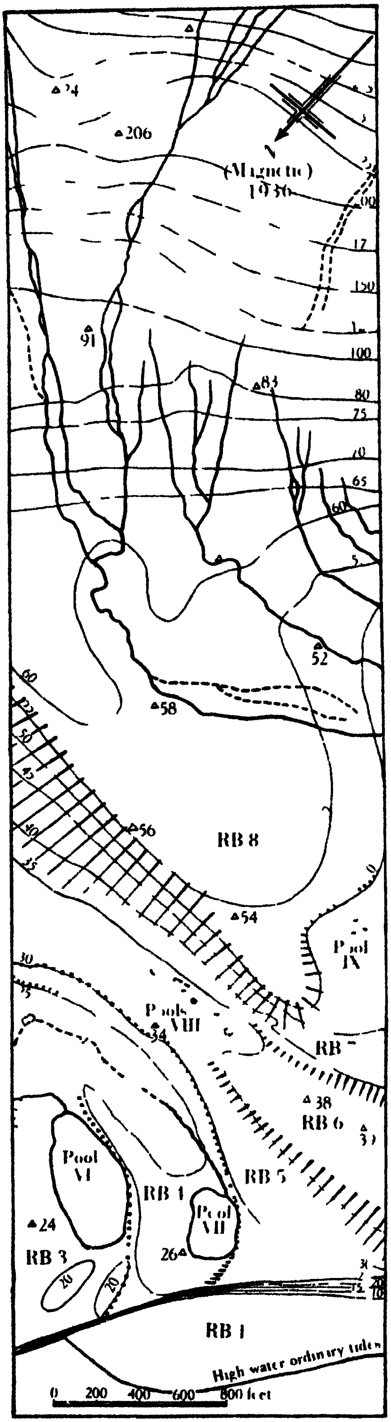

Fig 2*a*. Topographical survey

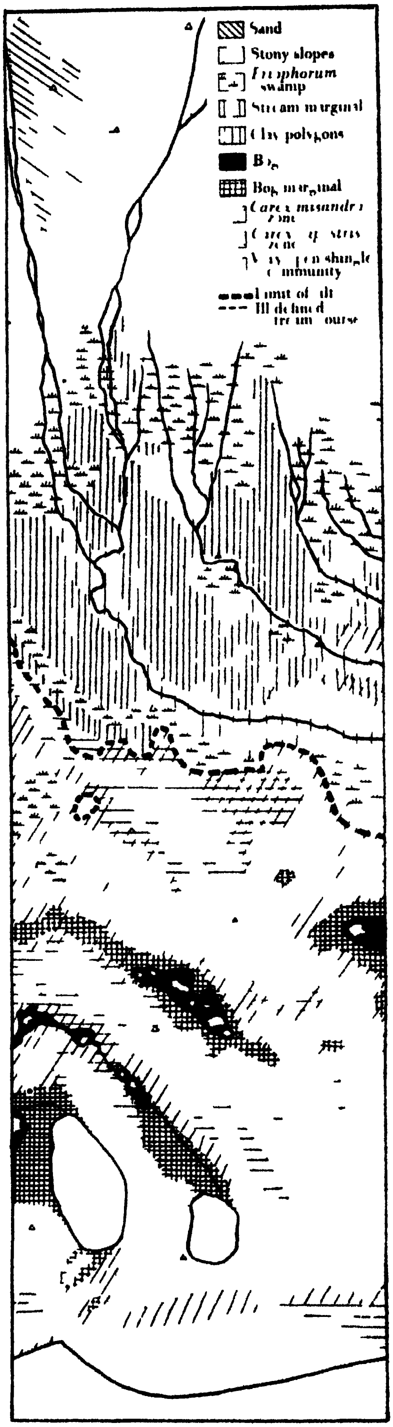

Fig 2*b* Distribution of vegetation

wet by seepage of water from round the base of talus cones and stable slopes which extend below the cliffs and loose screes of the mountains. There is a small sandstone outcrop at the inland end of the strip.

Thus four main habitat types are distinguishable:

(1) Shingle beach.
(2) Wet localities associated with pools and bogs.
(3) Silt, including stony mountain slopes.
(4) Sandstone.

As edaphic factors form the basis of this classification, examination of representative soil samples was undertaken to establish the more important physical and chemical characteristics of the soil types of the area under consideration. Methods and results are dealt with in § IV. It is clear that in their chemical composition, which is dominated by the high calcium carbonate content, the majority of the soils are substantially similar. Chemical differences are certainly not comparable with those between dolerite, sandstone, shale, gneiss, schist and limestone (Summerhayes & Elton, 1928; Michelmore, 1934). There are, however, marked mechanical differences between the soils of the different regions outlined above, which influence drainage properties, aeration and the availability of water and solutes (compare soils 1, 2 and 3 with 4, 5 and 6). The effect of chemical soil differences is illustrated by the sandstone outcrop (soil 7) which is surrounded on all sides by calcareous silt soils.

In the following account of vegetation the four main vegetation types correspond with the four habitat types, viz:

(1) Shingle beach communities.
(2) Bog community.
(3) Communities of silt.
(4) Vegetation of sandstone outcrop.

Methods in the study of vegetation

The distribution of the main vegetation types is shown in Fig. 2*b*. In view of the sharply defined zonation that is typical in high latitudes little difficulty was experienced in most cases in recognizing and delineating communities and the use of line boundaries is in general justified, but where sharp transitions do not exist interdigitation is indicated by superimposition of the hatching adopted for the respective communities. Some simplification has been resorted to in the interests of clarity.

As the object of this account is to indicate the interrelations of communities, individual units have not been described in great detail, but attention has been focused on physiognomy and its response to environmental changes. The individual plant communities studied occupy quite small areas in most cases, so that listing by general inspection was feasible and was preferred to examination of representative quadrats. Quantitative treatment was adopted in studying the interesting zonation of the shingle-beach vegetation. Frequency figures in Table 2 were obtained by Raunkiaer's method with a square sample $\frac{1}{10}$ sq. m. in area. Twenty samples in each zone were found to give a satisfactory indication of relative abundance; ten frequency classes are used. The symbol × signifies the presence of species in the community though not in the areas sampled. Where no frequencies are given (as in Table 1) × signifies the presence of a species. Frequencies denoted by letters are based on visual judgement. The lists do not represent actual transects, but are synthesized from data from representative communities arranged in suitable sequence to show the type of changes that occur in vegetation in response to a gradient in habitat conditions.

Degrees of cover were estimated by the use of a sampling area subdivided into 25; they are expressed as percentages. Cryptogams were not studied in detail. The more prominent species are listed together with their associates in the collected material.

More detailed consideration will now be given to the four edaphic regions and the plant communities which occupy them.

II. PLANT COMMUNITIES

(1) *Shingle beach*

Habitat.

The raised beach terraces have resulted from successive periods of slow and rapid emergence of the land at considerable time intervals and hence are of particular interest in providing vegetation and soil of progressively increasing maturity in natural sequence. The shingle is morainic material shaped by marine action and after elevation exposed to weathering mainly by frost. Soil 1 (p. 104) is shingle which has been elevated to about 30 ft. above sea-level and hence subjected for a considerable time to weathering; it is composed of irregular limestone pebbles with secondary calcium carbonate crystallization, together with fragments of schist and quartz. Stones range in size from chips and flakes retained by a 2 mm. sieve to stones of 10 cm. greatest diameter. The upper raised beach (RB 8) is considerably more weathered, the shingle is more sandy than in the lower beaches, and there is a quite high proportion of siliceous pebbles (soil 2); this is reflected in the *p*H of 7·0–7·7 as compared with 8·2 on RB 4. It is not certain that these differences are due solely to leaching, as it is quite possible that the type of beach material deposited has undergone a change in the considerable time interval that has elapsed between the deposition of the older and newer beach terraces. The heavily silted portion of RB 8 is considered as a separate edaphic region; towards the west end of the unsilted area and locally elsewhere there are signs that silting is extending, patches of silt giving the appearance of being injected into the surface soil from below. As usual in Arctic soils the influence of freezing is an important factor, as only the upper 2 to 3 ft. of shingle thaws out each summer. This has a uniform profile except for a humus gradient over the first 15–20 cm. and a moisture gradient towards the frozen subsoil. Where snow accumulates there is a dark surface horizon of varying thickness (soil 3 A) composed partly of lichen and phanerogam debris and partly of mud deposited by the melting snow. Such deposits contribute to the organic content of the underlying shingle (e.g. soil 3 B). A considerable protozoan fauna is reported for a similar soil near Bruce City, implying marked microbiotic activity (Sandon, 1924). The shingle in this area is in the main well drained and aerated, with a small fine earth fraction, so that root competition is severe; this may account for the fact that plant communities are open even in the most favourable localities, while very sparse vegetation reminiscent of that under desert conditions occurs where conditions are adverse. The vegetation of older soils is in some cases more closed than that on more recently elevated shingle, but, as will be seen, a far more important agent than soil maturity in differentiating vegetation is local variation in soil moisture and exposure, this apparently depending mainly on the degree of snow protection.

Vegetation.

The zonation of shingle communities. Four main zones have been recognized on the basis of the physiognomy and floristic composition of the shingle vegetation, cutting across the broad transition associated with habitat development.

(1) *Extremely open communities.* (*a*) Pioneer vegetation on newly elevated shingle. (*b*) On exposed dry shingle of older beaches. Open *Dryas* fjaeldmark poor floristically.

(2) Carex rupestris *zone.* Less open *Dryas* fjaeldmark with numerous additional species, notably *Carex rupestris.*

(3) Carex misandra *zone.* In moister localities, grading into (2) with greater floristic variety and abundance of *Carex misandra.*

(4) *Bog marginal.* Varied community in the wet region adjacent to bog areas. Some observations on pool-marginal vegetation are included.

More detailed consideration of these zones follows, with an indication of the influence of the environmental factors mentioned above.

Comprehensive species lists with frequency data from eighteen localities are collected in Table 2 (p. 93). The columns are arranged to illustrate the effect of the progressive improvement in habitat conditions on approaching large depressions. These changes were studied on the escarpment of the old shingle beach (RB 8), and on soils of intermediate age on RB 4 and RB 5.

(1*a*) *Pioneer vegetation on shingle.* Active beach building is in progress on RB 1 and at Cape Napier. Tidal and wave action in depositing the shingle results in a series of ridges and depressions at right angles to the direction of deposition (Dobbs, 1939). Newly exposed shingle consists of smooth flattened pebbles with a small sand and gravel fraction, but as secondary weathering proceeds the pebbles, as has been seen, become angular. Laminarian and fucoid remains form a drift line and yield, with marine plankton and driftwood, a small organic content.

In the colonization of new shingle on RB 1 crustose lichens are the pioneer plants: *Caloplaca elegans* (Link) Th. Fr. var. *tenuis* (Wbg.) Th. Fr., *C. murorum* (Hoffm.) Th. Fr. var. *obliterata* (Pers.) Jatta, *Polyblastia intercedens* (Nyl.) Lönnr., together with extremely sparse moss and deep-rooted phanerogams: *Saxifraga caespitosa*, *Minuartia biflora* and an occasional plant of *Saxifraga cernua*.

Colonization is mainly in the long depressions between beach ridges.

Sagina intermedia, *Minuartia biflora*, *Salix polaris*, *Cerastium alpinum*, *C. Regellii* and *Saxifraga oppositifolia* appear close behind the pioneer species, while in a moister area towards the high escarpment of the higher beaches, *Carex misandra*, *Deschampsia borealis*, *Juncus biglumis*, *Polygonum viviparum*. *Arenaria ciliata*, *Melandrium apetalum*, *Phippsia concinna* (Th. Fries) Lindb. and other species appear.

The moss flora of RB 1 is sparse, comprising in the main cushion-forming species in depressions; it includes:

Distichium montanum (Hagen) [=Swartzia montana]
Tortula ruralis
Bryum nitidulum Lindb. forma
Didymodon spitsbergensis Dixon (n.sp.)
Hypnum elodes Spr. forma[1]

The succession on the fairly moist shingle of RB 1 described above resembles that on the extremely dry exposed shingle at Cape Napier (see Dobbs, 1939) in the presence, as early colonizers, of *Sagina intermedia*, *Saxifraga caespitosa* and *Cerastium alpinum*. The following account of the vegetation of shingle may be regarded as dealing with later developmental stages in the community of unsilted beach terraces, although it must be borne in mind that there have been possible initial soil and climatic differences in the long period required for the extensive beach terraces to accumulate and become elevated, so that the flora of older beaches need not necessarily represent a later seral stage to that on newer beaches, although there is apparent continuity between the Cape Napier succession and the fjaeldmark of raised beaches 3, 4, 5, 6 and 7.

(1*b*) *Ridge and depression flora of dry exposed beaches*. The vegetation of the beach ridges of the main shingle plateau (RB 3, 4, 5, 6 and 7) is sharply differentiated from that of the swales. With a view to determining to what extent this can be attributed to exposure effects average wind velocities were measured with a hand anemometer, the vanes held a few inches above the ground surface, on a number of ridges and depressions on RB 4 and 5. These observations were made during a strong southerly wind with a velocity at 2 m. above the ground of 5–15 m./sec. Ground velocities on ridges were about 50 % of the 2 m. velocities, in depressions 13–40 % less than on ridges. As the Ice Fjord region of Spitsbergen is not subject to very high winds direct exposure effects in summer may be relatively unimportant, but drifting of snow into depressions at the onset of winter, with severe exposure only on ridges (Kihlman, 1890), under the wind velocity difference noted is probable (Braun-Blanquet, 1932). In the absence of observations during the winter the effects and distribution of snow have in the main to be inferred, but drifts were observed in depressions and in the lee of escarpments persisting into July, and it seems likely that ridges, mounds and the shoulders of escarpments are swept clear of snow at least part of the winter. In general, areas well protected by snow remain, on account of their topography, fairly moist during the summer and have therefore particularly favourable conditions for vegetation despite the slightly shorter growing period and lower soil temperatures as compared with dry exposed shingle (see p. 103), whereas elevated portions are liable to dry more rapidly.

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[1] According to Dixon the last form is similar to that collected by Walton from his zone 2 in the Cape Napier saltmarsh area.

On the beach ridges of the main beach plateau (RB 4, 5, 6 and 7, soil 1) there is a very open community (5–20 % cover) with large prostrate mats of *Dryas* accounting for about 80 % of the total phanerogam cover, orientated away from the ice cap, small clumped plants of *Saxifraga oppositifolia* and occasional wind-shaped tussocks of *Carex nardina*.[1] The shingle between is bare except for saxicole lichens on pebbles and a discontinuous lichen crust dominated by *Lecanora epibryon*.[2] *Cerania vermicularis* and *Cetraria nivalis* appear among *Dryas* stems (see Table 2, cols. 1–3).

The depression flora is conspicuously different, denser and floristically richer (25–40 % cover) with *Carex rupestris*, *Pedicularis lanata*,[3] etc. (Table 2, cols. 4–6). Mosses and lichens, particularly the fruticose forms *Cetraria nivalis* and *C. hiascens*, increase markedly. *Dryas* plants are smaller and closer together. There is usually a dark surface deposit on the soil.

The fjaeldmark on the weathered shingle (soil 2) on the exposed crest of RB 8 is of a less extreme type than that on newer beaches. There is more complete phanerogam (30–40 %) and lichen cover, and *Dryas* plants are smaller and more numerous (Table 2, col. 11). Beach ridges are not in evidence, but there are roughly polygonal shingle domes and, in the depressions between, a richer flora notable for the abundance of *Cetraria hiascens* and *Carex*

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[1] Other species occur locally, e.g. *Papaver radicatum*, but are not typical.

[2] *Lecanora epibryon* is certainly the dominant lichen in this region and not *L. tartarea* var. *frigida* as reported formerly.

[3] Root connexions were traced between the thick yellow roots of this species and the thin fibrous rootlets of *Dryas* and *Saxifraga oppositifolia*.

rupestris. Cassiope appears in similar depressions on moister parts of RB 8 (see Pl. 6, phot. 1, taken at the western end of RB 8). Measurements of wind velocity on the surface of a mound and in one of these depressions showed as much as 50% shelter in the hollows, where snow was observed persisting into July.

That soil modification due to physical weathering does not necessarily result in a more closed type of community is demonstrated on uneroded remnants of earlier raised beaches at the foot of the Campbell Range about 200 ft. above sea-level to the south-west of the survey area which support an extremely sparse *Dryas* fjaeldmark; these are very exposed, and dry during summer. It appears, therefore, under adverse conditions shingle vegetation is stabilized as very open fjaeldmark, but readily becomes more closed under more favourable conditions.

(2) Carex rupestris *zone.* The sharp differentiation of the vegetation of ridges, mounds and the shoulders of escarpments from that of beach depressions has been attributed mainly to exposure differences. A community resembling the depression flora occupies quite extensive areas not very dry in the summer and likely to be well protected by snow in winter, mainly in large shallow beach depressions, in the lee of escarpments, near the margins of the basins of bogs and pools, and on weathered shingle except where very exposed; note the distribution of *Carex rupestris* zone on Fig. 2*b*. Phanerogam cover is 30–40%, of which 45–60% is due to *Dryas*. *Carex rupestris* is a conspicuous member of the flora (see Table 2, cols. 7, 8), while the ground layer includes the striking *Bryum globosum, Lecanora epibryon, Cetraria* spp. and occasionally *Stereocaulon alpinum.*

(3) Carex misandra *zone.* Occupying similar situations but with a generally moister range a type of fjaeldmark may be distinguished in which there is a high representation of *Carex misandra.* This grades into *C. rupestris* fjaeldmark, and into bog-marginal communities at the wetter end of its range. Total phanerogam cover is 40–60%, of which *Dryas* accounts for 16–50%, whereas less xerophilous species such as *Salix polaris* increase as compared with the *Carex rupestris* type. Lichens are less conspicuous, but there are numerous cushion mosses notably *Encalypta commutata*; *Cassiope* is present in this zone, particularly round the base of the weathered shingle bank of RB 8 on soils with a dark surface accumulation indicative of snowdrifts (soil 3).

A generalized type of *Dryas* fjaeldmark is widely distributed in the Bruce City region on moist shingle as on the unsilted plateau of RB 8, on the extensive partially silted slope east of the bog systems, and on moist stable silt in the submontane region. *Carex rupestris* and *C. misandra* are prominent, also *Salix polaris,* while *Cassiope* is sometimes present (Table 2, cols. 9, 12). Summerhayes & Elton regarded this as the regional climax (1928, p. 283). It has been seen, however, that in more adverse localities there is a very open community which shows no evidence of passing to this more complex type.

Further, it is open to question whether areas like this, which have been subject to recent topographic change, have had time to develop a climax. The great variety of vegetation types is against this assumption.

(4) *Bog-marginal vegetation.* Hitherto shingle communities have been considered in which effects attributable to the duration of snow protection are reinforced by the influence of soil moisture content during the period of active growth. There can be little doubt that the depressions occupied by bogs and pools are fully protected by snow, so that differentiation of vegetation must be attributed mainly to factors operating in the growing season.

Bogs VII, VIII and IX occupy shallow depressions so that standing water is surrounded by a wet region with a high water table. Furthermore, small fluctuations in water level affect the water regime in the surface soil of considerable areas. Early in the summer the smaller pools are much more extensive than later. During July 1937, for example, the water level in pool VIII fell 6 in. As the summer advances, therefore, the surface horizon of regions towards the edges of the basin of the pools pass out of a waterlogged condition and become oxidized though still with a copious water supply. Peat does not form under these conditions, but a varied community characterized by sedges, grasses and large moss mounds. A number of characteristic communities is described below.

(*a*) On wet soils rarely actually flooded, as east of pools VI and VII, there is a rather open community with large tussocks of *Deschampsia borealis* and *D. alpina*, with *Salix polaris*, *Polygonum viviparum*, *Carex misandra*, *Juncus biglumis*, *Saxifraga aizoides*, *Equisetum variegatum* and considerable growth of moss. The soil may be shingle, or clay with sodden circular "polygons" (Pl. 7, phot. 4). *Nostoc* sp. is abundant. Wet clay areas, as near bog IX, may be colonized by *Dupontia Fisheri* and *Eriophorum Scheuchzeri*.

(*b*) Where there is a changing water table, or on soils kept wet by seepage of water round the base of an escarpment as above bogs VII and VIII, there are mounds and ridges of moss conspicuously colonized by *Carex parallela*, together with *Salix polaris*, *Carex misandra*, *Equisetum variegatum* and *Eriophorum angustifolium* (Table 2, col. 18); *Cassiope* is frequent on old shingle near bog VIII. *Dryas* accounts for less than 20% of the total phanerogam cover (*c.* 50%), and is confined to the dry crests of moss mounds which show a characteristic zonation of moss species, e.g. *Drepanocladus brevifolius* at the base and *Hypnum Bambergeri* and *Orthothecium chryseum* at the top.

(*c*) The vegetation of temporary pools affords a third type, as at the east end of bog VIII, where there are large moss tussocks with a coarse growth of *Carex saxatilis*. A loose mat of *Saxifraga oppositifolia* and *Salix polaris* straggling over a black surface horizon with wrinkled masses of *Nostoc*, occurs on temporarily flooded shingle north of bog VIII.

As the summer advances much of the bog marginal region becomes fairly dry.

Pool marginal vegetation.

The importance of soil moisture in differentiating shingle communities is further shown by the striking zonation surrounding the large pools (VI and VII). In addition, the pools are visited by numerous birds and are associated with local examples of nitrophilous moss community as on the north and east margin of pool VI and the east end of pool VII (see Walton, p. 120). Zonation on the steep shingle bank surrounding most of pool VII has been listed by Summerhayes & Elton (1923, p. 260). *Carex rupestris* and *C. misandra* should be substituted for "*Luzula confusa*" and *Lecanora epibryon* for "*L. tartarea*". The zones recognized by these workers do not seem to be typical. Table 1 has been compiled to show the salient features of the zonation on the steep shingle bank of pool VI near Bruce City - not subject to direct bird manuring.

Table 1

Species	1	2	3	4	5
Phanerogams:					
Cardamine pratensis	×	×	.	.	.
Dupontia Fisheri	.	×	.	.	.
Saxifraga Hirculus	.	×	.	.	.
S. cernua	.	×	.	.	.
S. aizoides	.	×	.	.	.
Polygonum viviparum	.	×	×	.	.
Juncus biglumis	.	×	×	.	.
Salix polaris	.	×	×		.
Cerastium Regellii	.	×	×		.
Draba alpina	.	.	×	.	.
Pedicularis lanata	.	.	×	×	.
Stellaria longipes	.	.	×	×	.
Carex misandra	.	.	×	×	.
C. rupestris	.	.	×	×	×
Saxifraga oppositifolia	.	.	×	×	×
Dryas octopetala	.	.	×	×	×
Carex nardina	.	.	.	.	×
Bryophytes:					
Drepanocladus revolvens	×	×	×		.
Chrysohypnum stellatum	×	×	×	.	.
Scorpidium turgescens	×	×	.	.	.
Bryum sp.	×	×	.	.	.
Ceratodon purpureum	.	×	.	.	.
Blepharostoma trichophyllum	.	×	.		.
Lichens:					
Lecanora epibryon	.	×	×	×	×
Cetraria nivalis	.	.	×		×
C. hiascens	.	.	×	×	.
Thamnolia vermicularis	.	.	.	.	×

Cryptogams are not recorded here in detail (see Summerhayes & Elton). Zone 1 is colonization of stranded plankton, 2 a wet moss zone above the general summer water level, 3 a band of dark hummocked lichen-covered soil, 4 a shingle zone covered with *Lecanora epibryon*, and 5 dry fjaeldmark of RB 4.

(2) *Bog*

The small moss bogs are in reality the marginal moss zone of small pools which has advanced forming a zone of shallow peat. This usually overlies a deposit of reduced grey mud containing sulphide (soil 4); the mud is strongly

Table 2. *Showing the changes in floristic composition and frequency in the transition from dry exposed shingle to the moist bog marginal zone*

Cols. 1–10 are for newer shingle on RB 4 and RB 5 and 11–18 for weathered shingle on the escarpment and crest of RB 8. Cols. 1–3, ridge flora; 4–6 depression; 7 and 8 and 11–13 *Carex rupestris* zone; 9 and 14–17 *Carex misandra* zone and 10 and 18 bog marginal.

Columns ...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Phanerogams:																		
Braya purpurascens (R.Br.) Bunge.	.	.	.	.	×	×	×	.	1		.	1	.	.	.	.	2	2
Cardamine pratensis L.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	×
Carex incurva Lightf. var. setina Christ.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	×
C. misandra R.Br.	.	.	.	3	1	.	7	5	7	3	1	9	4	7	6	8	8	8
C. nardina Fries.	2	2	×	1	3	.	.	.	.	.	×	.	.	.	.	.	.	.
C. parallela (Laest.) Sommerf.	.	.	.		.	.	.	.	.	4	.	.	.	.	.	.	.	4
C. rupestris All.	.	.	.	6	3	×	8	9	4	×	8	7	6	2	1	1	2	5
C. saxatilis L.		.	.	.	.	.	.	.	.	×	.	.	.	.	.	.	.	×
C. subspathacea Wormsk.	.		.	.	.	.	.	.	.	6	.	.	.	.	.	1	2	3
Cassiope tetragona Don.		.	.	.	.	.	.		×	.	.	1	2	2	4	5	2	3
Cerastium alpinum L.	.	.	.		.	.	.	.	.	.	.		.	.	.	.	.	.
C. Regelii Murb.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	1	.
Cochlearia officinalis L.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	×
Deschampsia borealis (Trautv.)		.		.	.	.	1	.	.	3	.	.	.	.	.		1	1
D. alpina (L.) Roem. and Schult.	.	.					.	.	.	×	.	.	.	.	.	.	.	×
Draba alpina L.			.	.	.	×	2		1	1	.	1	1	1	1	.	3	1
D. lactea Adams (= Wahlenbergii Htm.)				.	.	.	.	.	1	×	.	1	.	.		1		1
D. oblongata R.Br.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dryas octopetala L.	6	7	2	10	10	×	10	10	9	.	10	10	10	10	8	7	4	5
Dupontia fisheri R Br.		.		.			.	.	1	.	.		.	×	1	1	×	.
Equisetum variegatum Schleich		.		.	.	.	1	.	4	6	.	.	.	.	×	.	5	7
E. arvense L. var. alpestre Wahl.	.	.		.	.	.	.	.	×	4	.	.	.	.	.	.		×
Eutrema Edwardsii R.Br.	.		.		.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eriophorum angustifolium Rott. f. triste Th. Fr.	.			.	.	.	.	.	.	×	.		.	.	.		.	4
E. Scheuchzeri Hoppe	.	.	.	.	.	.	.	.	.	1		.	.	.	.	.	.	×
Juncus biglumis L.	.	.	.	.	.	.	2	×	2	5	.	×	1	1	2	×	5	6
Luzula nivalis (Laest.) Beurl	.	.	.	.	.	.	.	.	.	2	.	.	.	.		.	3	2
Melandrium apetalum (L.) Fenzl.		.	.	.	.		×	.	.	.	.	.	.	.		.	.	.
Pedicularis hirsuta L.		.	.	.	.	.	.		1	1	.				.	.	4	2
P. lanata Willd.	.	.	.	1	2		×	1	2	.	3	2	2	2	2	2	1	.
Polygonum viviparum L.		.	.		.	.	6	2	8	7	.	2	1	1	3	4	7	8
Ranunculus hyperboreus Rottb.	.	.			.	.	.	.	.	1	.	.	.	.	.	.	.	.
Salix polaris Wb.	.	.			.	.	6	×	4	8	.		×	1	3	4	10	9
Saxifraga aizoides L.	.		.	.	.	.	2	1	5	1	.	.	.	.	1	.	1	2
S. cernua L.	.	.	.	.	.	.	.	.	.		.	.	.			.	.	.
S. Hirculus L.	.	.			.	.	.	.	.	×	.	.	.	.	.	.	×	×
S. oppositifolia L.	10	10	10	10	10	.	10	10	8	5	10	10	10	10	10	10	8	10
Silene acaulis L.	.	.	.	.	.	.	.	×	.	.	2	1	.	.	.	.	.	.
Stellaria longipes Goldie	.	.	.	.	.	.	×	.	.	2	.	.	.	.	.	.	2	1
Percentage cover (phanerogams)	19	21	6	30	28	.	40	.	.	.	30	40	40	40	38	44	60	52

For explanation of frequency figures see p. 86.

Table 2 (*continued*)

Bryophytes in some of the communities 1–18

Column ...	2	7	8	10	14	17	18
Musci:							
Bryum globosum Lindb.	.	f.	r.	.	.	f.	.
Bryum sp.	×	.	.	.	.	.	.
Bryum sp.	.	.	.	o.	.	.	f.
Camptothecium nitens Schpr.	.	.	.	.	o.	o.	r.
Catascopium nigritum Brid.	.	.	.	o.	.	.	r.
Ceratodon purpureum	v.r.	v.r.	.	.	.	.	.
Chrysohypnum stellatum	.	.	.	o.	.	r.	o.
*Cinclidium stygium	.	.	.	f.	.	.	r.
Didtmodon spitsbergensis Dixon	.	f.	f.	.	f.	r.	o.
Distichium montanum Hagen	a.	.	.	r.	r.	.	v.r.
Ditrichum flexicaule Hpe.	.	r.	.	r.	o.	f.	o.
Drepanocladus lycopodioides var. brevifolius Berggr.	.	.	a.	f.	.	×	f.
D. revolvens (Sw.) Hedw.	.	.	r.	f.	.	.	o.
Encalypta commutata Br. Germ.	.	f.	.	a.	.	a.	a.
E. rhabdocarpa Schwgr.	f.	.	.	.	.	.	.
Fissidens osmundoides (Sw.) Hedw.	.	.	.	v.r.	.	.	v.r.
Hypnum Bambergeri Schpr.	.	a.	a.	o.	f.	f.	o.
H. pratense Koch	.	o.	.	.	.	.	.
Myurella julacea Br. Eur.	r.	.	a.	r.	.	v.r.	r.
Orthothecium chryseum Br. Eur.	.	.	.	a.	a.	f.	f.
Scorpidium turgescens (T. Jens.) Moenkem.	.	.	.	r.	.	r.	r.
Hepaticae:							
Blepharostoma trichophylla (L.) Dum.	.	.	.	.	×	.	.
Cephalozialla sp.	.	.	.	v.r.	.	v.r.	.

The Bryophyte flora was examined in a limited number of representative communities and collecting was not exhaustive.

* New record from Gips Valley by V. S. Summerhayes (see Dixon, 1922). It is fairly abundant as isolated stems in the material collected from the Bruce City region.

Lichen flora of shingle beaches

		I	II	III
	Caloplaca bracteata (Ach.) Jatta.	r.	o.	×
Sax	C. elegans (Link.) Th. Fr. var. tenuis (Wbg.) Th. Fr.	×	×	×
Sax	C. murorum (Hoffm.) Th. Fr. var. obliterata (Pers.) Jatta.	×	×	×
	Cetraria hiascens (Fr.) Th. Fr.	.	a.	a.
	C. nivalis (L.) Ach.	o.	a.	f.
	Cladonia lepidota var. stricta f. hypophylla Vain.	.	.	×
	Cl. pyxidata var. pachyphylla (Wallr.) Wain.	.	×	×
	Lecanora epibryon (Ach.) Ach.	d.	a.	a.
	L. (Aspicilia) verrucosa (Ach.) Laur.	×	×	×
Sax	*Lecidia elata Shaer.	×	×	×
	Ochrolechia upsaliensis (L.) Massal.	×	.	.
Sax	Polyblastia intercedens	×	×	×
Sax	Rhizocarpon geographicum (L.) DC, f. geronticum (Ach.) Th. Fr.	×	×	×
	Stereocaulon alpinum Laur.	.	×	r.
	Thamnolia vermicularis (Sw.) Ach. (=Cerania)	f.	.	.

Sax = Saxicole on pebbles.

The first column is based on a general collection of lichens from the dry exposed portions of raised beaches 4 and 5, while the second and third columns are for moister shingle communities associated with *Carex rupestris* and *C. misandra*.

There is a marked increase in abundance of fruticose forms on passing from exposed shingle with its flora of "wind lichens" (cf. Braun-Blanquet, 1932) to protected situations. The lichen flora seems to be substantially uniform throughout the area and is relatively poor in species, though it forms a general ground layer of considerable importance. The group was not worked in detail.

* With *Phaeospora parasitica* (Lonnr.) Arn. The first record of *Lecidia elata* as host of this lichen parasite.

calcareous (*p*H 8·2), while the top of the *Hypnum* peat is neutral or only slightly acid (e.g. *p*H 6·8). The term bog is therefore not entirely appropriate. As the summer advances there is a general fall in water level, shallower pools dry up and elevated regions of the bog become comparatively dry. Bird manuring is a complicated factor, as this is concentrated in the vicinity of pools, where birds collect to feed on planktonic organisms.

Vegetation.

Sphagna which occur in only a few localities in Spitsbergen (Summerhayes & Elton, 1928) are absent from the small alkaline bogs near Bruce City. The sodden brown *Hypnum* peat is matted with rhizomes of *Carex subspathacea*, *Dupontia Fisheri* and *Festuca rubra* forma. Other wet peat colonizers are *Eriophorum Scheuchzeri*, *Cardamine pratensis* and *Carex incurva* var. *setina*. *Eriophorum Scheuchzeri* and *Dupontia* form a prominent pioneer community fringing shallow pools. Zoned moss mounds up to 12 in. high which are a prominent feature of the bogs are occupied by *Salix polaris*, *Juncus biglumis*, *Carex incurva* var. *setina*, *Eriophorum angustifolium*, *Carex misandra*, *Polygonum viviparum* and occasionally *Dryas*.

Segregates of the genus *Hypnum* predominate in the moss flora. Below is a list with frequencies of mosses collected from a number of localities in bogs VII and VIII (Table 3).

Table 3

	1	2	3	4	5	6	7
Bryum obtusifolium Lindb.	.	.	l.a.	.	.	.	.
B. pseudotriquetrum	.	.	.	.	.	v.r.	.
Bryum sp.	.	.	.	.	.	o.	.
Calliergon trifarium Kindb.	.	a.	r.	r.	.	.	.
Chrysohypnum stellatum	.	.	f. l.a.	.	o.-l.a.	v.a.	v.a.
Cinclidium stygium	.	.	?	.	.	a.	.
Distichium montanum Hagen.	o.	.	.	.	.	.	.
Drepanocladus lycopodioides var. brevifolius Berggr.	a.	r.	v.a.	.	v.a.	a.	o.
D. revolvens (Sw.) Moenkem.	.	r.	.	o.	.	o. f.	o.
Fissidens osmundoides (Sw.) Hedw.	v.r.	.	.	.	.	.	.
Hypnum Bambergeri Schpr.	.	.	.	.	o.	.	.
H. turgidum	.	.	.	.	.	r.	.
Orthothecium chryseum Br. Eur.	.	.	.	.	.	r.	a. v.a.
Scorpidium scorpioides (L.) Limpr.	f.	v.a.	o. l.a.	d.	.	.	.
S. turgescens (T. Jens.) Moenkem.	.	.	.	.	o.	r.	.

Cols. 1–4 show the species in a number of sets of material collected from wet parts of bogs VII and VIII and 5–7 from localities not completely saturated (at the end of July 1937). Cols. 1 and 5 are for material collected in bog VII. The bogs described here have many features in common with Dobbs's "Wet Tundra", e.g. in the similarity of the moss flora, but the presence in the "Wet Tundra" of *Deschampsia borealis* (Dobbs, 1939, p. 139) suggests a closer resemblance to some of the communities classed as bog marginal in this account. Dobbs states (p. 140) that there is no extensive bog associated with the newer pools such as is found farther inland.

There is a succession of moss species as the surface of the bog is built up and the influence of telluric water is reduced. The main features of this succession at the present time seem to be:

Scorpidium scorpioides → *Drepanocladus lycopodioides* var. *brevifolius* → *Chrysohypnum stellatum* and *Orthothecium chryseum*.

Examination of five peat profiles along a transect in bog VIII threw light on the structure and development of the peat (see Table 4). These profiles were dug along a line passing through a drier hummocked zone near the edge of the central pool (profile I) towards the margin of the bog, including deep actively growing peat (II), the margin of a small pool (III), the bottom of this subsidiary pool (IV) and the shallow peat near the edge of the bog (V).

Table 4. *Moss species at different levels in a series of peat profiles in bog VIII*

	I	II	III	IV	V
Present vegetation:					
Chrysohypnum stellatum	a.	.	.	.	.
Drepanocladus brevifolius	f.-a.	.	.	.	d.
Ditrichum flexicaule	o.	.	.	.	.
Orthothecium chryseum	r.	.	.	.	.
Drepanocladus revolvens	f.	r.	.	.	.
Scorpidium scorpioides	v.r.	d.	d.	.	r.
Aneura pinguis	r.-o.	Peat growing	Peat growing	Submerged	.
	Eroded, no peat formation				
Peat—Top:					
Chrysohypnum stellatum	v.a.	.	v.r.	.	.
Drepanocladus brevifolius	o.	.	v.a.	v.a.	d.
Orthothecium chryseum	a.-v.a.	.	.	.	.
Drepanocladus revolvens	o.	a.	a.	.	.
Calliergon giganteum	v.r.	.	.	v.r.	.
C. trifarium	Leaves and twigs of *Salix polaris* and *Dryas*	f.	.	.	.
Scorpidium scorpioides	.	r.	o.	f. ?	.
S. turgescens	.	.	.	f.	.
Middle:					
Chrysohypnum stellatum	v.a.	.	.	.	.
Drepanocladus brevifolius	r.	v.a.	v.a.	.	.
Calliergon giganteum	? f.	.	.	.	.
Scorpidium turgescens	f.	.	.	.	.
	Peat badly preserved much monocotyledon debris and *Equisetum*				
S. scorpioides	.	.	.	.	.
Drepanocladus revolvens	.	.	.	.	.
Base:					
Drepanocladus brevifolius	v.a.	v.a.	.	v.a.	v.a.
D. revolvens	f.	.	.	o.	.
Scorpidium scorpioides	o.	v.a.	.	.	×
S. turgescens	.	.	.	o.-f.	Much decomposed

Peat is about 30 cm. deep in profile I, 20 in III, and 12 in V.

Drepanocladus brevifolius is the dominant form in the bulk of the peat. There is some indication of *scorpioides* peat beneath the main layer of *brevifolius* peat in profiles I, II and V, but decomposition has advanced too far for certainty. Largely submerged and invading the fringe of pools is a coarse growth of *Scorpidium scorpioides*, and the new growth in profiles II and III is dominated by this species. This new growth of *scorpioides* growing unconformably on *brevifolius* peat, and the occurrence in profile IV of entirely submerged *brevifolius* peat at the bottom of a shallow pool are of particular interest, suggesting either a wetter recent climatic period, or an elevation of the water-level in the bog by building up of the peat surface round the central pools and an overflowing of these pools to resubmerge the former bog surface, thus creating suitable conditions for recommencement of the *scorpioides* → *brevifolius* succession.

Bird manuring:

Elevated portions of bogs VIII and IX have been influenced considerably by bird manuring which has resulted in strikingly differentiated mounds usually bright green or golden brown in colour, contrasting with the dull brown of unmanured peat. These consist mainly of thick cushions of *Aulocomnium turgidum*, *Mnium affine* and *Orthothecium chryseum*. Bryophyte species collected from five localities subject to manuring are listed below (Table 5).

Table 5. *Bryophyte species from manured sites in bog VIII*

Musci:					
Amblystegium serpens	.	.	v.r.	.	.
Aulocomnium palustre Schwgr.	v.r.	.	.	.	.
A. turgidum Schwgr.	d.	.	.	.	.
Brachythecium turgidum (Hartm.) Harton.	.	.	.	d.	f.
Bryum cernuum Hedw. (= B. pendulum Hedw.)	.	.	v.r.	.	o.
B. obtusifolium Lindb.	.	.	.	.	o.
*Calliergon giganteum (slender form)	.	.	.	r.	.
Catascopium nigritum Brid.	.	.	o.	.	.
Camptothecium nitens Schpr.	.	f.	.	.	a.
*Chrysohypnum stellatum	r.	o.	v.a.	r.	v.a.
*Drepanocladus revolvens	.	.	.	r.	.
Mnium affine Bland.	.	.	.	r.	d.
*Orthothecium chryseum	.	v.a.	.	.	o.
Hepaticae:					
Alicularia scalaris	.	.	v.r.	.	.
Blepharostoma trichophyllum	.		v.a.	.	
Cephalozia sp.	.		v.r.	.	.
Cephaloziella sp.	.	.	a.	.	.
Lophozia sp.	.	.	v.r.	.	.

Species marked with an asterisk are present in unmanured bog.

(3) *Silt*

General characters of the region. Large talus cones have accumulated in a regular series of gorges cut into the soft gypsiferous cliffs at the foot of the Campbell Range. A portion of one of these fans is included at the southern corner of the tract under discussion. Drainage water from the mountains forms lateral streams, or seeps out round the base of the talus cones where the angle of slope is rapidly decreasing, forming a number of streams which have transported large quantities of silt or clay, derived from weathering of soft sedimentary rocks, over the back of the raised beach plateau. Interaction between erosion and silting results in changes in the course of the streams with complicating effects on the ecology of the region. The silt is highly calcareous with up to 60% of calcium carbonate (soil 6).

The most important factors differentiating communities are the water regime and relative permanence of the soil. The silted region is characteristically moist owing (*a*) to its position and origin, (*b*) to the moisture-retaining properties of the soil. The latter statement requires some qualification. Reference to the mechanical analysis data for soil 5 shows that there is an appreciable "clay" fraction (33%), but the clay, as is predictable from its origin by secondary physical weathering, is not highly colloidal. In consequence the drainage properties of the soils resemble those usually associated with silt more closely than those of highly dispersed clay. Some of the silt soils dry out to form crumb-like aggregations, but these are readily reduced to fine powder by pressure. In this dry state the surface is caked hard and cracked on account of shrinkage contrasting with its condition in spring and early summer when the silt is in a very soft plastic condition as shown on slopes by evidence of solifluction in the shape of stone stripes and elongated polygonal areas. The seepage zone at the base of the slopes is kept permanently swampy by flushing of snow water and there is a wet fringing region along stream courses. But elevated areas between the streams are well drained so that the soil dries out and becomes aerated, with parallel effects on the vegetation. Transitions from aquatic and semi-aquatic communities to those of drained sites were studied on:

(1) the nearly level silted portion of raised beach 8;

(2) the rising ground at the foot of the screes and outwash slopes.

There is a marked difference in the physiognomy of the communities owing to the stony character of the upland region.

	Wet	Drier
Silted beach	Stream marginal	Polygonal clay flat
Upland (stony)	Eriophorum swamp	Stony silt slopes, and talus fans

Stream marginal communities.

(*a*) On the nearly level silted beach newly deposited silt in shallow slow-moving portions of streams is invaded by ***Eriophorum Scheuchzeri*** and ***Dupontia Fisheri*** which catch transported silt. ***Eriophorum angustifolium*** comes behind these (Table 6, col. 1).

(*b*) Along fairly permanent stream courses continually saturated fine silt deposited in backwashes forms accumulations of strongly reduced grey sul-

Table 6. *Species present in silt communities*

The columns are general lists for communities with visually judged frequencies. Cols. 1–3 are for stream marginal vegetation, 4 fissure polygons, 5 *Eriophorum* swamp and 6–8 upland communities.

	1	2	3	4	5	6	7	8
Braya purpurascens	.	.	r.	r.	.	.	.	.
Carex misandra	.	.	o.	f.	o.	o.	o.	
C. parallela	.	.	.	.	l.a.	l.	.	.
C. rupestris	.	.	.	.	.	o.	.	.
C. saxatilis	.	.	.	.	l.	.	.	.
C. subspathacea	.	d.	.	.	.	.	.	.
Cassiope tetragona	.	.	.	.	.	v.r.	.	.
Cerastium alpinum	.	.	.	.	.	.	r.	o.
C. Regellii	.	.	.	.	.	.	.	r.
Deschampsia borealis	.	l.	o.	o.	r.	v.r.	v.r.	.
Desch. alpina	.	.	v.r.	.	.	.	.	.
Draba alpina	.	.	r.	r.	.	r.	r.	.
Dryas octopetala	.	.	o.	d.	.	d.	d.	r.
Dupontia Fisheri	f.	l.	.	.	o.	.	.	.
Equisetum variegatum	.	.	.	.	f.	l.	.	.
E. arvense var. alpestre	.	.	.	.	.	r.	.	.
Eriophorum angustifolium	o.	l.	.	.	f.	l.	.	.
E. Scheuchzeri	f.	f.	.	.	f.	f.	.	.
Eutrema Edwardsii	.	.	.	.	.	v.r.	.	.
Juncus biglumis	.	o.	f.	r.	f.	r.	.	.
Luzula nivalis	.	.	.	.	.	r.	.	.
Melandrium apetalum	.	.	.	.	.	.	.	r.
Papaver radicatum	.	.	.	.	.	.	.	r.
Pedicularis lanata	.	.	.	.		r.	.	.
P. hirsuta	.	.	.	r.	.	.	r.	.
Polygonum viviparum	.	.	f.	o.	f.	o.	.	.
Salix polaris	.	o.	f.	f.	f.	o.	o.	.
Saxifraga aizoides	.	.	.	.	v.r.	r.	r.	o.
S. Hirculus	.	.	.	.	.	v.r.	.	.
S. oppositifolia	.	.	o.	f.	r.	f.	a.	r.
Stellaria longipes	.	.	.	.	.	r.	.	r
Bryophyta:								
Bryum globosum	.			.	.	o.	.	.
B. pauperidens Dixon (sp. nov.)	.	.	.	.	r.	.	.	.
Bryum sp.	.	f.	.	r.	r.	.	.	.
Brachythecium turgidum (= nitens)	.	.	.	o.	.	.	.	.
Camptothecium trichodes	.	.	.	o.	r.	.	.	.
Catascapium nigritum	.	v.a.	.	.	.	.	.	.
Chrysohypnum stellatum	.	.	.	.	o.	.	.	.
Didymodon spitsbergensis	.	.	f.	f.	o.	.	.	.
Distichium montanum	.	.	o.	.	r.	r.	.	.
Ditrichum flexicaule	.	.	.	r.	r.	.	.	.
Drepanocladus lycopodioides var. brevifolius	.	r.	.	r.	l.a.	.	.	.
D. revolvens	.	.	o.	.	l.	.	.	.
Encalypta alpina (= E. commutata)	.	.	.	a.	o.	o.	.	.
Hypnum Bambergeri	.	.	f.	f.	r.	f.	.	.
H. pratense	.	.	.	.	r.	.	.	.
H. turgidum	.	.	.	.	r.	.	.	.
Myurella julacea	.	.	.	.	r.	.	.	.
Orthothecium chryseum	.	l.f.	.	.	.	o.	.	.
Plagiothecium flexicaule	.	.	r.	.	.	.	.	.
Scorpidium scorpioides	.	l.f. .	.	.	l.	.	.	.
S. turgescens	.	.	o.	o.	o.	.	.	.
Trichostomum fragile	.	.	.	.	r.	.	.	.
Hepaticae:								
Cephalozia sp. (single stem)	.	.	.	.	.	×	.	.

Lichens. A mainly sterile pioneer lichen community is widespread on silt. *Lecanora epibryon*, with some *L. verrucosa*, is the commonest species. *Caloplaca bracteata*, *Cladonia pyxidata* var. *pachythallina*, *Cetraria nivalis*, and *C. hiascens* are present in comparatively developed communities. As on shingle, lichens are subordinate to phanerogams in determining the physiognomy of vegetation.

phide mud, matted with a fibrous mass of rhizomes and roots of *Carex subspathacea*. Slow seasonal silting results in a gradual elevation and diggings show a banded profile, with black fibrous horizons alternating with layers of fine silt. The *Carex* rhizomes grow upward to keep pace with silting (Table 6, col. 2). The dominance of *C. subspathacea* recalls bog vegetation also arising on reduced clay deposits. Moss cushions are built up and in places include *Scorpidium scorpioides* and *Drepanocladus lycopodioides* var. *brevifolius*, the principal constituents of active bog peat, although these are also common on wet aerated soils.

(*c*) Flanking the larger streams in places is a belt of deep silt only sparsely colonized. Sodden in early summer it dries out with marked shrinkage later in the season. *Salix polaris*, *Juncus biglumis*, *Polygonum viviparum*, *Deschampsia borealis* and, in drier localities, *Dryas* form a very open vegetation cover (Table 6, col. 3). The soil surface is covered with a wrinkled sterile lichen crust (? mostly *Lecanora epibryon*). In older areas moss mounds are built up and the soil surface shows signs of polygon formation as described below.

Polygonal flat.

Higher portions of the silt deposit between stream courses support a well-established fjaeldmark community characterized by the presence of contiguous fissure polygons (see Huxley & Odell, 1924), the domed cracked centres of which are practically bare and vegetation is confined to the depressions so that it forms a network, covering about 20%. The deep fissures separating polygons are filled with a humus soil. The marginal flora is dominated by *Dryas* in drier localities and *Salix* in moister (Table 6, col. 4). Succession on fissure polygons and on the stream marginal silt deposits described above (*c*), from which the polygonal type seems to develop, is considered to be held up by the hard caked condition of the soil at the end of the growing season. Soils from both these localities have a mottled profile suggestive of gley formation and seem to be alternately reduced and oxidized each season (soil 5) (see Pl. 6, phot. 2).

Stony silt vegetation.

Eriophorum *swamp*. Recently transported stony silt, kept permanently wet by percolating water, is practically bare in places except for colonizing *Eriophorum Scheuchzeri*. On more permanent areas there are zoned moss mounds and ridges conspicuously colonized by *Carex parallela*, *Salix*, both *Eriophora*, *Juncus biglumis*, etc. (Table 6, col. 5). There is a considerable evidence of solifluxion. In the diffuse course of a slow-moving stream along the seaward margin of the silted flat polygons with stony margins are present resembling bog marginal polygons, with an *Eriophorum-Deschampsia* community and moss mounds.

Stable slopes. (i) Moist stable slopes above the swampy zone support a *Dryas* fjaeldmark resembling floristically the *Carex misandra* type on shingle, with a fairly rich phanerogam flora and prominent moss and lichen flora. The latter includes *Lecanora epibryon*, *Cetraria hiascens* and *Bryum globosum*. In physiognomy this community differs from its shingle counterpart mainly in the presence of large irregular stone blocks. In places there are isolated clay polygons (Table 6, col. 6).

(ii) Between the talus cones and below the unstable screes that cover most of the mountain range are outwash slopes with a high proportion of silt; the angle of slope is less than the rest angle of the screes. *Dryas* rooted between stone blocks creeps over them to form large mounds. *Hypnum Bambergeri* and other mosses form moss cushions with *Salix* and *Carex misandra*. Solifluxion is occurring on some of these slopes and soil is organized into alternating bands of silt and stone longitudinal to the slope with vegetation largely confined to the latter, the silt belts are practically bare except for a sterile lichen crust (Huxley & Odell, 1924) (see Pl. 7, phot. 3).

Talus cones. On stable talus material with silt round the base of the fans there is a somewhat similar flora to that described above (i), though sparser because of a higher proportion of stone blocks. In places there are stone-clay polygons and stone semicircles (Huxley & Odell) (Table 6, col. 7).

Much less developed communities occupy stonier disturbed material nearer the apex of the fans, characterized by colonizing species such as *Cerastium alpinum*, *C. Regellii*, *Melandrium apetalum* and *Saxifraga aizoides*, cf. the colonization of moist shingle on RB 1 (Table 6, col. 3).

Large clumps of *Saxifraga aizoides* are present on wet stony silt near the lateral drainage streams (soil 6).

A very large portion of the fans towards their apex consists only of jumbled stone blocks devoid of vegetation.

(4) *Sandstone outcrop*

The vegetation of the outcrop is interesting in illustrating the effect of soil composition. Two regions are conveniently recognized:

(1) Stable to the west.

(2) Sand slide to the north.

(1) On the stable sandy soil (soil 7) is an old community with *Cassiope* associated with

Carex misandra
Dryas octopetala
Oxyria digyna
Saxifraga aizoides
S. oppositifolia
Silene acaulis

(2) Loose sand is quite bare. *Braya purpurascens* with long superficial roots longitudinal to the slope is an early colonizer. Where more stable *Carex misandra*, *Polygonum viviparum*, *Draba alpina*, *Melandrium apetalum*, *Saxifraga oppositifolia*, *Papaver radicatum*, *S. caespitosa*, *Luzula nivalis*, *Pedicularis hirsuta*, *Deschampsia borealis* and *Dryas* form a moist open community.

The presence of *Cassiope* and the acidophilous *Oxyria digyna* is significant (cf. Scholänder, 1934) as the former species is absent from the surrounding calcareous silt soils, and the latter was not found anywhere else in the vicinity of Bruce City.

III. FLOWERING SEASONS

Some data were collected on the flowering season (in 1937) of the most prominent species. These observations showed that flowering of species is more advanced by about a fortnight in dry fjaeldmark than in moist localities on silt or shingle. *Saxifraga oppositifolia* and *Draba* species were in full flower at the beginning of July and had finished flowering by the end of the month on the dry raised beaches. *Dryas* flowers about two weeks later. By the middle of July *Carex* species were in panicle over the whole area.

A few late-melting snow patches enabled the effects of snow lie to be observed. Three plots were kept under observation and the percentage of individual plants of *Dryas* and *Saxifraga oppositifolia* flowering was noted at intervals. Plot 1 was completely snow-covered at the beginning of July and completely exposed by July 12. It was on well-insolated, fairly moist shingle. Plots 2 and 3 were completely free of snow in early July, on well-drained exposed shingle. The results are summarized graphically in Fig. 3. The fourth diagram in Fig. 3 is a record of soil temperatures at a depth of 5 cm. on plots 1 and 2 and of air temperature, with the earlier part of the record in sufficient detail to show diurnal fluctuations. A consistently lower temperature in the moister soil is apparent.

Rapid onset of flowering after snow melting, shortness of the flowering season, and staggering of the seasons of the two species are points clearly brought out by this study.

IV. SOIL INVESTIGATION

Methods

Collection of samples. Soil samples were collected on the same day (10 August 1936) in metal containers and sealed with air-tight lids as laboratory investigation had to be postponed for several weeks. Samples were collected from the horizon most completely exploited by fine rootlets (usually the upper 3–6 in.). To reduce sampling error a number of samples from each region was put together and mixed before examination.

Investigation of samples. This was carried out in the Department of Soil Science, Oxford. I wish to thank Mr G. R. Clarke and Dr J. Russell for valuable advice.

(i) *Field water content.* Soil was heated for 48 hr. at 100° C. The weight of stones subsequently removed was subtracted from that of total soil and water content expressed as percentage of the fine earth dry weight.

(ii) *Mechanical analysis.* By the Sudan Method (Wright, p. 43), 5 g. of dry fine earth was investigated.

(iii) *p*H. Field determinations were made with the B.D.H. capillator.

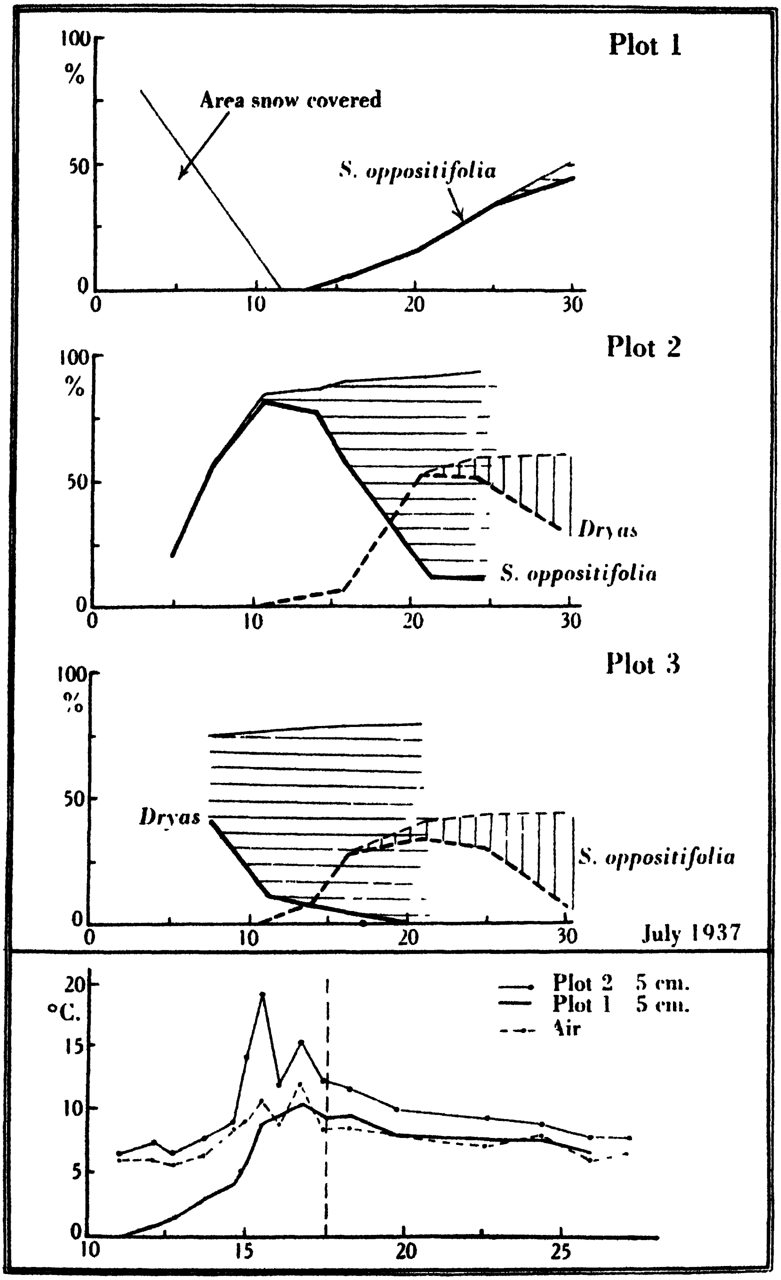

Fig. 3. Data for the percentage of flowering individuals of various fjaeldmark species on different dates in July, 1937 (abcissa). The shaded zones indicate the proportions of withered flowers the lowest graph the soil and air temperatures.

(iv) *Calcium carbonate estimations.* 2–3 g. fine earth ground in a mortar to pass a 100-mesh sieve. CO_2 loss on treatment with HCl in a Schroeter apparatus calculated as calcium carbonate.

(v) *Soil carbon.* By the method of Walkley & Black. Results multiplied by the conventional factor (1·724) to convert to organic matter.

(vi) *Total nitrogen.* By micro-Kjeldahl method of Chibnall & Westall. I am indebted to Mr G. C. M. Harris of the Department of Botany, Oxford, for these determinations.

(vii) *Mineral nutrients.* A few tests were applied for soluble nitrogen and phosphorus employing the Universal Soil Testing System (Morgan, 1935).

(viii) A few field tests were carried out to establish qualitatively the state of oxidation of the soil. Freshly collected soil samples were dissolved in dilute HCl to bring the iron into solution and sodium thiocyanate solution added. Formation of a red compound indicates the presence of ferric iron and shows that the soil is oxidized, while failure to produce a red colour is evidence that the soil is reduced, with iron in the divalent condition.

Soil data

	Soil no.							
Data	1	2	3 A	3 B	4	5	6	7
Field moisture content (% fine earth dry wt.)	12	6	88	33	—	19	20	16
Mechanical analysis:								
% total soil dry wt. stones	87	70	26	82	4	—	--	--
% fine earth dry wt.:								
Coarse sand	17	77	6	45	23	7	1	26
Fine sand	61	14	56	33	45	34	80	59
Silt	6	4	6	5	17	26	12	4
"Clay", i.e. colloids	16	5	33*	18	15	33	7	11
*p*H (colorimetric)	8·1	7·7	7·4	7·7	8·2	8·2	8·4	7·4
$CaCO_3$ content of fine earth % dry wt.	37	16	12	26	17	28	62	2
Soil carbon (as organic matter) % fine earth dry wt.	5	2·5	20	9	1·5	2	0	6
Total nitrogen % fine earth	—	0·08	0·7	0·08	0·2	0·12	0·06	--
Mineral nutrients (Morgan colour tests):								
Soluble nitrogen	Low	Low	Med.	Med.	Low	V. low	Low	Low
Phosphorus	Low	Low	Med.	Med.	Low	V. low	Low	Low

* In the case of 3 A there is probably quite a high proportion of humus colloids contrasting with the preponderantly mineral skeletal soils which characterize this region.

V. DISTRIBUTION OF *CASSIOPE TETRAGONA*.

The Klaas Billen Bay region gives opportunities for studying the occurrence on calcareous soils of *Cassiope tetragona,* which is a species of calcifuge tendency. Damp weathered shingle on RB 8 (*p*H 7·0–7·7) supports the only extensive *Cassiope* community in the surveyed area. Local patches occur on newer beaches in sheltered situations and on the sandstone outcrop (soil 7). There is particularly luxuriant growth immediately surrounding erratic schistose boulders which are scattered over the raised beach terraces, whereas the strongly alkaline relatively impermanent silt soils are unsuitable.

The general conclusion reached was that *Cassiope* can compete successfully on alkaline soils satisfying the following requirements:

(1) Well protected by winter snow cover.
(2) Moist.
(3) Some humus accumulation.
(4) ? Stable.

Soil 3 is typical of denser *Cassiope* communities on calcareous shingle.

VI. SUMMARY AND CONCLUSIONS

In describing a sample of the vegetation of calcareous soils in the arid interior region of Spitsbergen an account has been given of shingle silt and bog communities and their habitat relations. The open vegetation of shingle and drier silt belong to the general type of Arctic vegetation called "fjaeldmark", while bog and wet silt communities are examples of "wet tundra" (Summerhayes & Elton, 1923, p. 216). This account therefore describes local examples of two broad types of community.

Fjaeldmark. Open vegetation on shingle seems to be primarily determined by climatic influences and by the stony nature of the soil, and graded into zones by exposure and moisture effects depending on snow cover and relief. Examination of species lists shows that phanerogam and cryptogam floras are substantially similar on the two soil types, though silt communities are more varied and floristically poorer individually as is predictable from their more temporary character. On dry shingle invasion and colonization proceed extremely slowly apparently limited by the slow process of soil development, whereas silt deposited in a highly comminuted form permits of more rapid transitions. Because of the unstratified nature of vegetation succession is rudimentary. Fissure polygons on silt retard development and partly through soil heterogeneity give rise to striking hyperdispersion, paralleled to some extent in banded communities on ridged shingle beaches and uneven vegetation on polygonal weathered shingle, where differential snow protection seems to be the determining factor. It is not possible to point to a definite climax community, though *Dryas* fjaeldmark with *Cassiope tetragona* on weathered shingle is probably the most developed fjaeldmark.

Wet tundra. In wet situations, mechanical features of the substrate again exert little influence on the species range. Although *Eriophorum Scheuchzeri* and *Dupontia Fisheri* colonize both stream margins and the margins of shallow bog pools, the subsequent succession seems to be strongly influenced by soil aeration. *Hypnum-Carex subspathacea* bogs have arisen on waterlogged soils in large depressions, while stagnant stream marginal areas likewise tend to *Carex subspathacea* turf formation. On the other hand, silt and shingle areas kept permanently wet by flushing with fresh water, wet aerated shingle and shingle with a high fluctuating water table have open communities notable for the presence of sedges and grasses. Of considerable interest is the fact that the shallow *Hypnum* peat in the bogs is stratified in a manner recalling the regeneration complexes of *Sphagnum* bogs.

Summerhayes & Elton (1928, p. 256) have drawn attention to the paucity of the flora in Klaas Billen Bay as compared with other inner fjord regions. Notable species absent from the area are *Empetrum nigrum*, *Rubus chamaemorus*, *Betula nana*, *Vaccinium uliginosum* and *Sphagnum* species. The poorness of the soil and its high calcium carbonate content, dryness, and exposure due to the proximity of the inland ice sheet may be responsible for this.

General features of the vegetation worthy of mention are the relative unimportance of cryptogams in determining the physiognomy of most of the communities, contrasting in this respect with the predominantly lichen and moss communities in, for example, the metamorphic region of north-west Spitsbergen. The extreme scarcity of Hepatics, except in elevated moss cushions of manured bog, may be attributed to the prevalent alkalinity. The abundance and variety of Carices is noteworthy compared with the prevalence of *Luzula confusa* on non-calcareous soils (cf. Scholänder, 1934). Extensive search failed to reveal the presence of this species near Bruce City in 1936 and 1937. It was found in a few non-calcareous sites round Petunia Bay. However, distribution studies on Carices, Gramineae and Juncaceae in Spitsbergen are too incomplete to permit of confident generalizations.

ACKNOWLEDGEMENTS

Taxonomic determinations were made by the following:

Phanerogams: at the Royal Botanic Gardens, Kew, and by the author. Mosses and hepatics by Dr E. W. Jones with confirmations by H. H. Dixon. Lichens by I. Mackenzie Lamb of the British Museum. I wish in addition to thank Mrs R. G. Taylor for her competent assistance in the field work.

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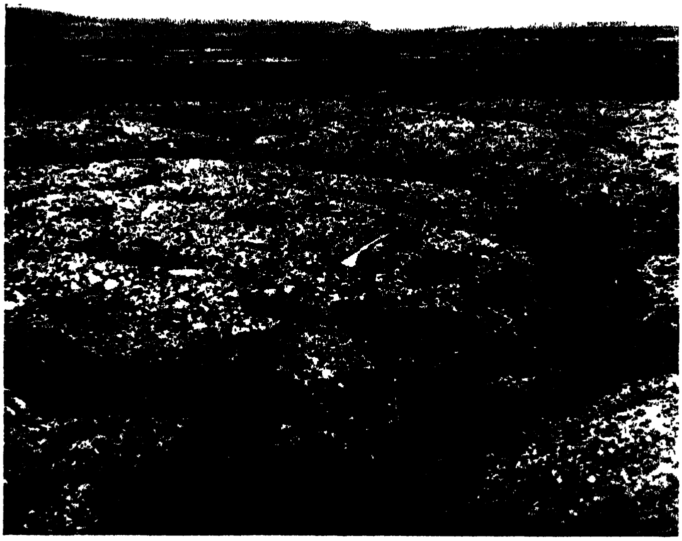
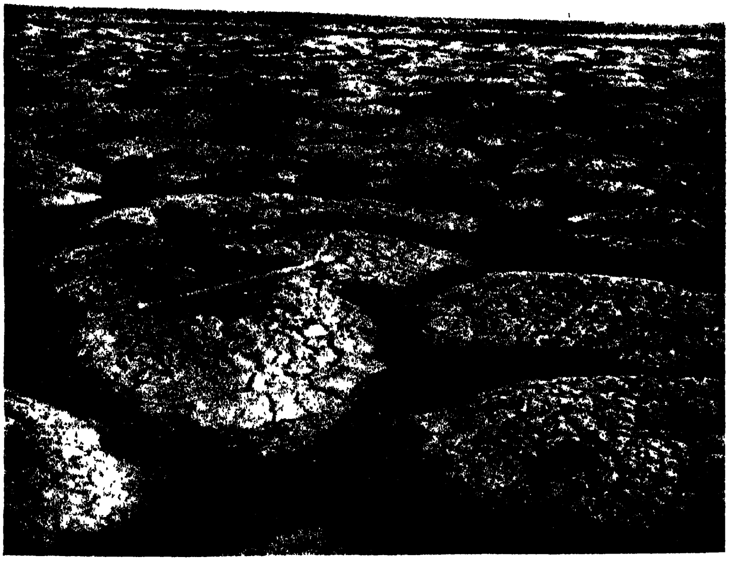


Phot. 1. Large shingle "polygons" on weathered shingle, with *Cassiope* prominent in the depressions.



Phot. 2. Fissure polygons on silted beach plateau with *Salix polaris* dominant in the foreground

Phot. 3. Stone stripes on silt slope. *Dryas* occupies the stony bands and a sterile lichen crust the silt areas.

Phot. 4. Old mud polygons near Pool IX (cf. Dobbs, Phot. 6) *Eriophorum Scheuchzeri* and *Dupontia Fisheri* are conspicuous.

A STUDY OF THE ROOT SYSTEM OF THE BEECH IN WOODLAND SOILS, WITH ESPECIAL REFERENCE TO MYCORRHIZAL INFECTION

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(*With one Figure in the Text*)

1. Root systems and rooting depth

It is well known that the root system of beech shows a certain plasticity in form according to the type of soil on which it grows. In all localities, however, young seedlings are alike in having a long tap root which comprises the main part of the system. The length of time that this root remains functionally important varies with conditions, especially those arising out of soil variations. Vater (1927) described the root system of beech in Germany, and pointed out that the trees he studied retained their tap roots up to the age of 27 years. As the trees aged, however, the long surface branches became increasingly more important as absorbing organs, and at 80 years shallow outgoing branches of the heart root comprised the greater part of the functional root system. Hilf (1927) also made a study of beech-root systems, noting that in adult trees the system was shallow with occasional deep sinkers. As a rule the majority of the shallow roots remained inside the canopy of the aerial branches of well-grown trees. In soils derived from Bunter sandstone showing litter and humus accumulation, young roots tended to grow upwards and colonize these highly organic surface layers. They also colonized pockets of humic matter derived from the decay of old roots in the soil. Hilf gives interesting data upon the percentage of roots in soil horizons. 77 % of the fine roots were found in the humus layer, while 23 % were found in the top 50 cm. of mineral soil. 12 % of the large roots were present in the humus, and 88 % in the mineral soil.

Watt (1934) has described the roots of beech in the Chilterns and pointed out that in deep soils of the plateau with little humus accumulation the roots go relatively deep, whereas in plateau soils where raw humus accumulates, the majority of the fine roots are to be found in the surface layers.

The first study of beech woods in the Chilterns has allowed a classification of the root systems to be made. There are two main types. The first includes shallow root systems which are not only found on soils which are morphologically shallow, but also on raw humus soils which may be described as physiologically shallow. The second type includes deep root systems on the deepest soils of the escarpment and the better plateau soils.

2. SUBJECTIVE OBSERVATIONS

(*a*) *Shallow root systems*

The shallow soils in beech woods on the chalk escarpment are usually bound together with fine roots. The majority of these roots show secondary thickening. In the spring, young growing tips are found abundantly, especially in the surface layers (8 cm.) of the soil. Root growth seems to be considerably restricted by drought, and it is difficult to find growing apices during the late spring and early summer. Mycorrhizal rootlets are always small and invariably poorly branched. They occur throughout the soil but are especially frequent in the surface layers. In places where litter accumulates in depressions, the superficial organic layer is colonized extensively by the apices of long roots in the spring, and mycorrhizas are more actively formed.

The latter condition is characteristic of soils on which raw humus accumulates, and which are consequently physiologically shallow. Here, as Hilf has pointed out, the root system is almost restricted to the upper layers of the soil. The whole humus layer is bound together with fine roots. At the base of this horizon there are abundant fine roots, the majority of which show secondary thickening, and bear as branches dead mycorrhizal systems which become black. Above this, the upper layers contain many primary long roots, with long white apices. giving rise behind to branches some of which pursue a course of unrestricted growth, but the majority become infected with mycorrhizal fungi and produce extensive systems of mycorrhizal roots. In the latter, the leader is not only long, but bears many branches which increase in length from the distal to the proximal end. These systems are brown in colour, often having whitish apices to each branch. They have been described as the pyramidal type of mycorrhiza (Harley, 1937).

Many long roots are found in the uppermost layers of relatively undecayed leaves. Colonization of these layers takes place rapidly in January or early February, as soon as root growth begins, and all but a very thin surface layer is held together by beech roots. Mycorrhizal infection of the branches of these long roots takes place in early summer.

The soil below the humus is almost lacking in unthickened roots. Only rarely are growing apices or mycorrhizas encountered, except in pockets of humic material. The colonization of pockets of humic material is also noticeable in podsolized soil. Here the B horizon contains a small number of active roots, whereas they are markedly lacking in the leached A horizon.

Drought has a very adverse effect on the roots in the humus layers of these soils. The litter and humus readily dry out in dry seasons, and the roots they contain become dead and shrivelled. It is notable that mycorrhizal roots are not so readily injured by drought as uninfected apices. This might, other conditions being equal, constitute a beneficial effect of mycorrhizal infection upon tree growth. In this connexion it is interesting that Cromer (1935), writing in Australia on the significance of mycorrhiza in *Pinus radiata*, suggested that drought caused a collapse of the cortex of uninfected absorbing roots but not of mycorrhizal roots. He, too, suggested drought resistance as a possible property of the fungal sheath advantageous to the host plant.

(*b*) *Deep root systems*

In deep soils in which decomposition of the humus is rapid, the soil becomes stained with incorporated organic matter. The fine roots show little tendency to be restricted to the surface layers, and the soil is not so intensely exploited by roots as in the types mentioned above. Active roots are frequently found throughout the top 20 in. (49 cm.) but are only concentrated near the surface in localities where more humus accumulates than usual. The laterals are not nearly so heavily infected with mycorrhiza, and the branch systems which retain many active apices, have been described as the diffuse type of mycorrhiza. Locally, where the litter is deep, there is a repetition of conditions found in raw humus soil.

3. QUANTITATIVE OBSERVATIONS

The following table gives examples of the weights of roots in the upper layers of several Chiltern soils. Each was chosen as a fair sample of one of the types described above. The figures are fresh weights of roots in the top 8 in. (20 cm.) of soil, obtained by dissecting blocks of soil 6 in. (15 cm.) square.

Table 1. *Fresh weights (g.) of roots in Chiltern soils*

Shallow soil of escarpment 8–10 in. deep (*ca.* 20–25 cm.)	Deep escarpment soil 15–20 in. (*ca.* 36–49 cm.)	Deep plateau soil, no raw humus	Raw humus soil of plateau
(1) 126·44	(1) 35·59	(1) 21·72	(1) 53·45
(2) 100·89	(2) 40·21	(2) 18·31	(2) 54·00
(3) —	(3) 46·41	(3) —	(3) —

The largest weight of roots was found in the top sample of very shallow escarpment soil. This is a reflexion of the fact that the whole depth of the rooting medium was sampled. It indicates a complete exploitation of the soil by the roots. The deeper escarpment soils have less than half this weight of roots in the top 8 in. Since the trees here are usually better developed and more vigorous, it is reasonable to assume that the total quantity of roots is not actually less, but that they are spread completely over a greater depth of soil. The deep plateau soil may be viewed in the same light, for the trees are more vigorous and the soils very much deeper. The high values found in raw humus soils which bear trees of poor vigour, are attributable to the concentration of roots into the surface layers with high organic content.

A comparison was made between the two types of plateau soil by dissecting out the roots, horizon by horizon. Table 2 gives the depth of each horizon as well as the fresh weight of roots, and the fresh weight of roots per inch, in the upper layers of soil of each type, from two localities bearing mature beech wood.

Table 2. *Distribution of roots*

Type of soil	Depth of horizon in.	Nature of horizon	Fresh weight (g.) of roots per layer	Fresh weight (g.) per inch
Raw humus present	0·5	Litter	0·99	2·0
	1·0	Raw humus and humus stained	18·05	18·1
	1·5	Leached layer	9·76	6·5
	5·0	Subsoil	24·65	4·9
Raw humus present	0·25	Litter	0	0
	1·5	Raw humus and stained soil	25·5	17·0
	2·0	Mottled and leached	6·9	3·5
	4·0	Subsoil	5·1	2·6
	4·0	Subsoil	5·0	2·5
	4·0	Subsoil	2·6	1·3
Rapid litter incorporation	0·25	Litter	0·5	2·0
	2·0	Humus stained	6·1	3·1
	6·0	Slight stains of humus	15·2	2·5
Rapid litter incorporation	0·25	Litter	0·3	1·2
	2·0	Stained	3·1	1·6
	6·0	Slightly stained	15·1	2·5

The figures in Table 2 lay particular emphasis on the correlation between the accumulation of incompletely humified organic matter, and the concentration of roots in the soil horizon. Nevertheless, they give an unsatisfactory picture of the true differences between the roots of beech on different soil types. No conception of the variation in structure of the roots can be obtained from them.

It has been previously indicated (Harley, 1937) that the nitrogen content of various types of fine roots, both infected and uninfected, depends upon their structure. Mycorrhizal roots contain more nitrogen per unit dry weight than uninfected roots, and roots showing secondary thickening have very low nitrogen contents. Table 3 gives a summary of nitrogen analyses of fine roots of beech drawn from several localities.

Table 3. *Nitrogen contents of roots in mg./g. dry wt.*

	Uninfected	Diffuse	Pyramidal	Coralloid	Nodules	Loose weft	Secondary types	Secondary thickening	Dead mycorrhizas
(1)	18·6	28·8	26·9	22·8	17·3	24·6	26·4	12·5	15·0
(2)	17·8	21·2	25·4	22·7	12·6	23·4	20·0	12·0	—
(3)	14·7	21·2	24·3	—	11·7	—	—	9·9	—
(4)	18·3	28·0	24·4	—	—	—	—	9·0	—
(5)	14·6	28·0	20·1	—	—	—	—	8·3	—
(6)	18·0	22·3	29·3	—	—	—	—	—	—
Mean	17·0	24·9	25·1	22·8	13·9	24·0	23·2	10·3	15·0

Putting any other significance of these figures on one side, they provide, at this point, a means of checking the observations on the amount of mycorrhizal roots on various soils. The commonest types of mycorrhiza (cols. 3 and 4, Table 3) have a nitrogen content sufficiently different from uninfected and secondary thickened roots, to allow the nitrogen content of roots in the various soil horizons to be used as an estimate of amount of infection. Table 4 gives estimates of the nitrogen content of the fine roots of the top 8 in. of three types of soil.

Table 4. *Nitrogen content of root systems, mg./g. dry wt.*

Escarpment soil Calcareous, no humus accumulation		Plateau soil No humus accumulation			Plateau soil Raw humus accumulation	
	N in mg./g. of roots		N in mg./g. of roots			N in mg./g. of roots
Horizon		Horizon	(a)	(b)	Horizon	
Litter	21·2	Litter	21·4	20·1	Litter	20·4
Soil	8·6	Humus-stained soil	12·3	11·2	Raw humus	18·9
		Subsoil	9·8	5·4	Leached	12·3
					Subsoil	13·8

The roots from the litter zone of all these soils, have a similar nitrogen content of about 21 mg./g. Here there are no roots showing secondary thickening, hence approximately 50% of the roots by weight are infected. However, the litter accumulation is not constant on the three soils, but usually in the following increasing order of accumulation: escarpment, plateau soil with rapid incorporation, and raw humus. Therefore, assuming that wherever litter lies it is equally exploited by roots, one may conclude that the raw humus soil contains most roots of this highly infected type. The raw humus layer of this latter soil again contains roots of high nitrogen content, of 18·9 mg./g. The lowest percentage of infected roots by roots by weight to explain this figure would be 25%, on the assumption that all the uninfected roots were unthickened and had a nitrogen content of 17 mg./g., and that there were no dead mycorrhizas present. This assumption of course is not valid, so that the humus layer must contain more than 25% of infected roots, a value not found in any horizon (except the litter) of any of the other soils.

The remaining layers of all the soils have roots whose nitrogen contents indicate that a very large number of them are secondarily thickened. The subsoil of the raw humus soil shows values which possibly may indicate the presence of a certain percentage of infected roots, but the subsoils of the escarpment and better plateau must be mainly colonized by thickened roots.

These results fall into line extremely well with the qualitative observations on the amount of infection on these three soil types.

4. THE SIGNIFICANCE OF THE HIGH NITROGEN CONTENT OF INFECTED ROOTS

In assessing the significance of the high nitrogen content of infected roots as compared with that of uninfected roots consideration must be given to the nitrogen content of the soil. Analysis of the total nitrogen content in milligrams per kilogram of dry soil excluding loose leaf litter are given in Table 5, col. 2.

Escarpment soil contains more than four times as much as the plateau soils which are very similar. These results are explicable as the resultants of incorporation of nitrogen into the soil, the drainage from the soil and the uptake into the plants upon them. The escarpment bears a vegetation of poor vigour upon a soil in which the disappearance of litter is very rapid. The raw humus soil bears a vegetation of somewhat similar vigour on a soil in which much nitrogen is locked in the unincorporated litter. The better plateau soil bears a vegetation of great vigour upon a soil in which the litter disappears rapidly. As might be expected, the total nitrogen of the soil bears no relation to the nitrogen content of the root system nor to the amount of mycorrhizal infection. These two characters of the root system do, however, bear a relation to the extent of humus incorporation which may be measured quantitatively by the carbon/nitrogen ratio of the soil (Table 5, col. 4) and to the rate of formation of soluble nitrogen fractions by the soil (see Table 5, cols. 5–12). As may be seen, the amount of mycorrhiza increases as the carbon-nitrogen ratio increases. That is as the extent of humification of organic matter decreases. In the escarpment soils the C/N ratio approximates to that of humus itself (Waksman, 1936). Here mycorrhizas are least in evidence. On the other hand the organic matter in raw humus soils is relatively little changed and mycorrhizas are very abundant.

Table 5. *Analysis of Chiltern beechwood soils. Analytical values in mg./kg. of dry soil*

Soil	Total N	Total C (CO_3 excluded)	C/N	N total soluble at sampling	N total soluble after incubation	NO_3 at sampling	NO_3 after incubation	NH_4 at sampling	NH_4 after incubation	Rest of soluble N at sampling	Rest of soluble N after incubation
Escarpment	4892·4	53,165	10·87	100·0	137·0	35·9	79·0	15·2	7·6	49·1	50·4
Plateau without raw humus	1186·9	21,290	17·94	37·6	57·5	11·9	20·5	16·6	17·1	9·1	25·1
Plateau with raw humus	1212·8	39,985	32·97	49·7	45·1	16·4	9·3	14·8	10·8	18·5	19·9

Similarly, the extent of mycorrhiza formation decreases with the rate of mobilization of nitrogen, and rate of nitrification in the soil. Hence the high nitrogen content of mycorrhizal roots is not related to ready availability of nitrogen in the soil, but the reverse.

These observations do not go far in simplifying the problem of the significance of mycorrhiza, for this reason: it is usual for the mycelium of fungi to have a nitrogen content per unit weight much greater than that of uninfected roots. They may be as great as 60 or 70 mg./g. dry weight. The high nitrogen content of infected roots might therefore be a reflection of the mere presence of a sheath of fungal material of high nitrogen content about the roots, a point that requires investigation. It is possible nevertheless that there is a readier absorption by mycorrhizas from soil where nitrogen is present mainly in organic combination. To test this, analyses have been performed on the buds of adult trees.

5. THE NITROGEN OF BUDS OF ADULT TREES

The resting winter buds were chosen as readily detachable organs, which might be assumed to vary in both size and nitrogen content according to the supply of nitrogen from the soil. Samples were taken of apical buds from lateral branches under the canopy up to 7 ft. from the ground. The two localities chosen for sampling were: (A) chalk escarpment wood, soil 6–8 in. deep, and (B) plateau wood, on soil showing deep accumulation of litter and raw humus. The height of the trees and the closeness of the canopy were as far as possible similar. The buds were removed, divided into samples of 100, dried at 100° C., weighed, and the total nitrogen content estimated. There were twenty-three samples from the plateau wood and ten from the escarpment wood. The results are given in Table 6.

Table 6. *Analysis of buds*

	Weight of 100 buds in g.		Mg. N per 100 buds		Mg. N per g. dry weight	
Locality	Mean	Limits	Mean	Limits	Mean	Limits
Chalk escarpment soil	1·923	1·173–3·176	29·37	25·57–34·57	17·03	13·01–23·21
Plateau soil with raw humus	1·415	1·112–1·975	21·24	17·00–27·55	15·11	12·79–17·12
Significance of difference between means	Sig. $P > 0{\cdot}05$	—	Sig. $P > 0{\cdot}01$	—	Insig.	—

The buds of the escarpment soil are of greater dry weight than those of the plateau. Correlated with this, the nitrogen content per bud is also greater. The difference between the means of nitrogen per g. dry weight is not significant.

It is possible therefore that the size of the buds from trees on the raw humus soil may be actually limited by nitrogen supply, so that the low dry weight may be a consequence of low N supply. The increased availability of nitrogen in the escarpments is then reflected in larger buds, rather than in increase in nitrogen per unit weight of buds.

6. THE NITROGEN OF LEAVES OF ADULT TREES

The analysis of leaves leads to similar conclusions, although the data are based on fewer analyses. A comparison was made between leaves produced in high and in low light intensity in the two localities sampled for buds. The results are given in Table 7.

Table 7. *Analysis of leaves*

Locality	Light % of daylight	Dry weight 50 leaves in g.	mg. N per 50 leaves	mg. N per g. dry weight
Escarpment	15	1·6116	37·81	23·54
Escarpment	22	3·7886	57·28	22·91
Raw humus soil	12	1·3201	23·31	17·70
Raw humus soil	32	1·9468	37·94	19·42

An estimate of the errors of sampling was obtained by considering the variation of five samples from escarpment soil at low light intensity, and this was found to be small enough to allow the following deductions to be made.

The leaf weight of the trees on the two soils is similar, within the bounds of error, at low light intensities. But at high light intensities the weight of escarpment leaves was more than doubled, whereas those of the plateau increased by only 50%. The nitrogen content per leaf from trees of the escarpments is much greater in both low and high light intensities than that of leaves of trees from the plateau soils. The increase of nitrogen per leaf was, within the bounds of error, proportional to the dry weight increase in both cases.

To sum up the evidence of the last two sections: it seems reasonably certain that the nitrogen supply to the trees on chalk escarpment is greater than to those on raw humus soils. This then may be correlated with greater nitrogen content of the soil, greater rate of litter incorporation and greater rate of nitrogen mobilization. It is not correlated with infection, for infection is greatest on raw humus soil. There is no evidence however that infection does not increase nitrogen absorption. Nevertheless, if infection does increase nitrogen absorption, it does not overcome completely the poor rate of supply resulting from the slow rate of incorporation of litter on raw humus soils.

7. MYCORRHIZAS AS AN INTEGRAL PART OF THE SOIL SYSTEM

These results give the evidence upon which part of the Preliminary Note (1937) was based. The outstanding feature to be observed is that the estimation of the amount of root infection on the three soils studied in detail is placed on an objective basis by the use of the nitrogen contents of the roots as a measure of infection. The evidence agrees so entirely with the subjective observations, that this aspect of the problem affords a firm basis for work.

The results, briefly stated, are that mycorrhizal infection is more abundant on poor soils where the C/N ratio remains high, and the rate of mobilization of nitrogenous material and nitrification are low. Hatch, working on *Pinus* (1937), has also stressed this point. He found that mycorrhizas were "produced in abundance under conditions of low availability of four elements: nitrogen, phosphorus, potassium, and calcium, or lack of balance in the availability of these elements". He points out that there has been a tendency to stress the possibility of mycorrhiza having an effect on nitrogen economy, whereas his own results show that the increase of root surface brought about by mycorrhizal infection increases the ease of absorption of soil nutrients in general.

These conclusions might well apply to the mycorrhiza of beech, for in the natural "beech" soils here studied low availability of mineral elements is correlated with the slow breakdown of organic matter, and high C/N ratios. Estimates of available calcium were made by leaching soil with NaCl solution, and of the other elements by Morgan's colorimetric tests (Morgan, 1935) on the identical soil samples used above. The results are presented in Table 8.

Table 8

	Ca mg. equiv. 100 g. air-dry soil	K	PO_4	Fe″	Fe‴
Escarpment	45·38	+	+ + + +	Very slight trace	Trace
Plateau, no raw humus	2·72	+ + +	+ + +	+	+ +
Plateau, deep raw humus	2·22	Trace	+ +	+ + +	+ + + +

The raw humus soil in which mycorrhizal roots are very abundant is therefore characterized by low calcium and potassium a smaller available phosphorus content than elsewhere. and finally a high concentration of ferrous iron, which indicates conditions detrimental to plants. The other two soils, in which less mycorrhizal infection is found, are more balanced in mineral composition. Raw humus accumulation and the correlated phenomena of high C/N ratio and low nitrogen availability, seem to be related to this mineral composition. Estimates made on the same three soil samples show that both bacterial and fungal numbers are correlated remarkably closely with litter breakdown. Table 9 gives counts of these organisms by the plate method, after suitable dilution of the fresh soil.

Table 9. *Micro-organisms in soil. Numbers per gram of dry soil*

Soil	Bacteria in millions	Fungi in thousands
Chalk escarpment	25·4	114·9
Plateau soil, no raw humus	18·8	60·9
Plateau soil with raw humus	2·4	48·4

It cannot be claimed that these results are any more than rough estimates of the true numbers of bacteria and fungi present. For many micro-organisms are either unable to develop, or develop very slowly upon the media used. Nevertheless, they do give an estimate of the activity of the microflora of the soils. It therefore seems certain that mycorrhizal development is intimately related with the important soil activities, and this is stressed by a study of Fig. 1. Here the relation between available calcium (graph 3), nitrogen mobilization, nitrate formation (graph 1), bacterial numbers, and fungal numbers (graph 2) are shown plotted against the C/N ratio. which may be used as a measure of litter incorporation. A curve is also shown representing the number of mycorrhizal roots per cent of the total roots in the top 8 in. of

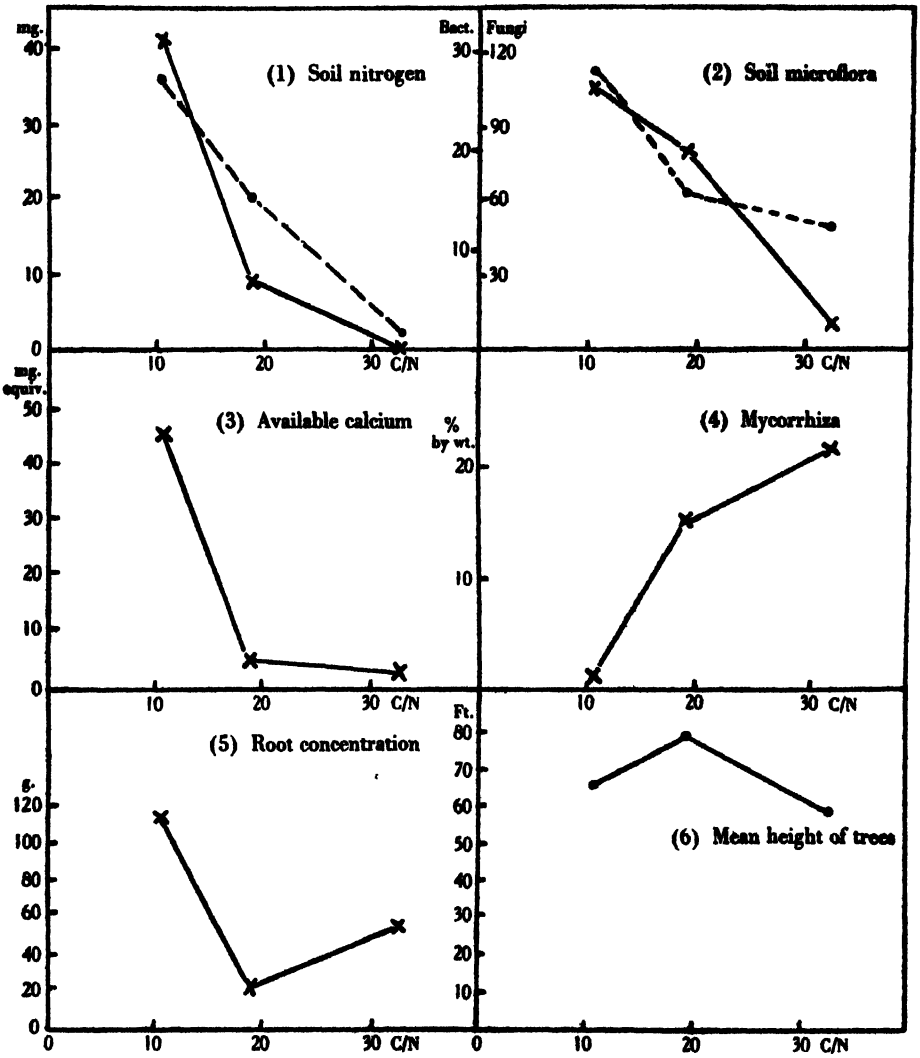

Fig. 1. Graphs showing the relation between soluble nitrogen (1), soil micro-organisms (2), available calcium (3), mycorrhiza (4) and concentration of roots (5) in the top 8 in. of soil and the extent of incorporation of organic matter with the soil as measured by carbon/nitrogen ratio. Data concerning the heights of trees derived from the papers of Dr A. S. Watt are shown for comparison in graph 6. Graph 1, increase on incubation of ×——× nitrate and ●---● total soluble nitrogen in mg. per kg. dry soil. Graph 2, number of bacteria in millions ×——× and fungi ●---● in thousands per g. of dry soil. Graph 3, available Ca. in mg. equivalents per 100 g. of dry soil. Graph 4, mycorrhiza calculated as percentage by weight of roots in top 8 in. of soil. Graph 5, weight of fine roots in top 8 in. of soil area of block 6 × 6 in. Graph 6, mean height of trees in ft. Each point represents the mean of a group of woods on similar soil types (Watt, 1934).

soil (graph 4). These figures were obtained from the nitrogen analyses of roots dissected from blocks of soil, together with subjective data, and although not such exact analyses as the others, accurate in so far as the data allow.

It is therefore apparent that the extent of mycorrhiza formation is a function of the soil system, and must be viewed in that light.

The variation in vigour of beech growth on this range of soil types brings a further variable under consideration. On soils where mycorrhizas are abundant, the vigour of the trees is poor; at the other end of the range, where mycorrhizas are few, trees of the same order of vigour are found. Intermediate soils, in which mycorrhizas are present but not in great abundance, bear trees of greatest vigour. These variations in vigour, then, are not primarily attributable to differences in mycorrhizal equipment, or conditions affecting the formation of mycorrhizas, but to the available rooting depth of the soil. This point is stressed in graphs 5 and 6 in Fig. 1, showing rooting depth of beech as measured by concentration of roots in the top 8 in. of soil, and height growth of the trees derived from the data of Watt (1934). The latter are not derived from the exact localities in which soils and roots were examined, but are means of his measurements for trees on soils of those types.

Furthermore, analyses of buds and leaves have shown that nitrogenous substances seem to be more available on the escarpment soils, which have high rates of nitrogen mobilization and fewer mycorrhizal roots than raw humus soils which have slow nitrogen mobilization and large numbers of mycorrhizal roots. The effect of the mycorrhizas on the absorption of nitrogen does not therefore equalize the availability of this element on these two widely differing soils. No real evidence has therefore been obtained as to the correctness of what Hatch has termed "The organic nitrogen theory of mycorrhizas". Therefore the problem is being attacked in greater detail, by means of a series of pot experiments, the results of which it is hoped will be available during the next year.

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STUDIES IN SALT-MARSH ECOLOGY

SECTIONS VI AND VII. COMPARISON WITH MARSHES ON THE EAST COAST OF NORTH AMERICA

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(*With Plates* 8 *and* 9 *and fifteen Figures in the Text*)

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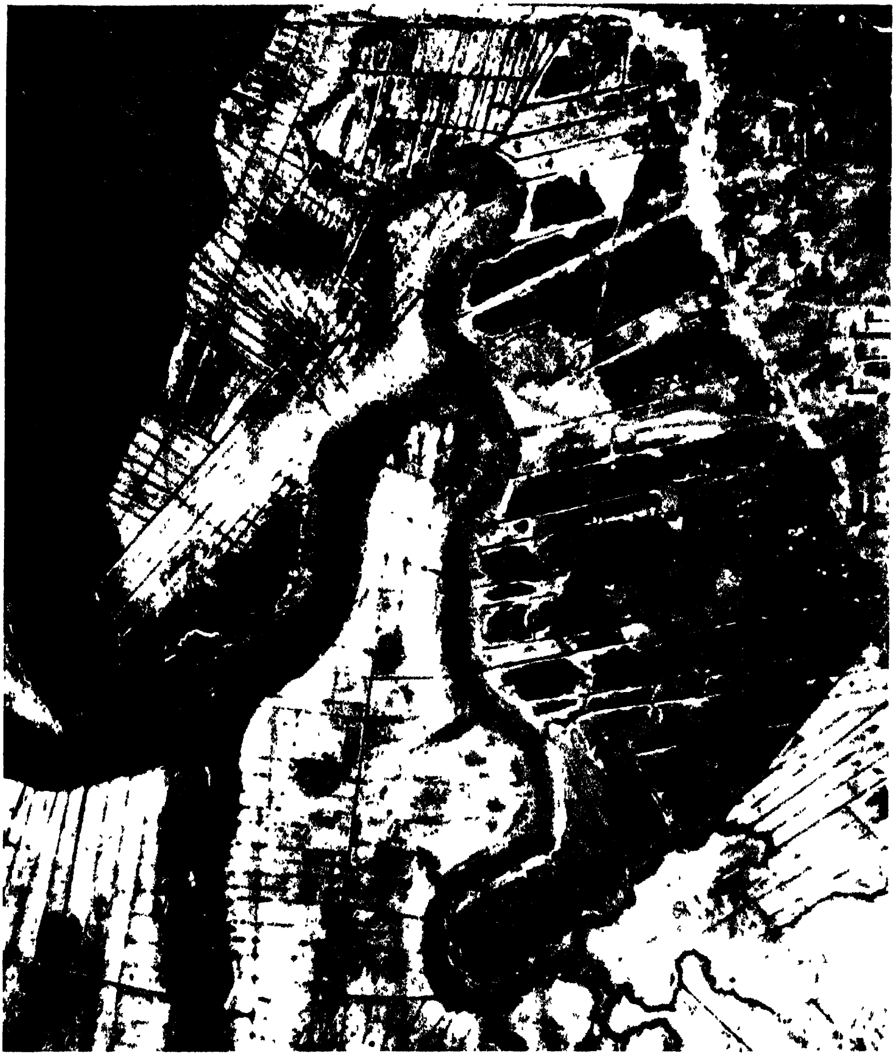
VI. Environmental factors

Introduction

During 1935–6 the writer was the holder of a Henry Fellowship at Harvard, and whilst there carried out a study of the salt marshes of New England. In particular a single large marsh, Romney or Lynn Marsh, near Boston, Mass., was selected for the more intensive work in the same way that the salt marshes of Scolt Head have been investigated in Norfolk. In spite of the fact that the New England marshes differ very widely from those of Norfolk, nevertheless there are certain features in which there is a marked similarity, and it is the purpose of these two sections to emphasize both these aspects. The major factors operating on a salt marsh have already been discussed (Chapman, 1938*a*), but as time precluded the collection of data about all these factors the following five were selected, on the basis of previous experience in Norfolk, as being the most important:

(1) Tides.
(2) Water-table.
(3) Drainage.
(4) Aeration.
(5) Salinity.



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Phot. 5. Distribution of the phanerogams on part of Romney Marsh near Oak Island.

● Juncus Gerardii. δ Spartina alterniflora. / Limonium trichogonum.
○ Triglochin maritimum. ∵ Salicornia and Suaeda. G Glyceria maritima.
P Plantago oliganthos. ‖ Spartina patens. = Distichlis spicata.
// Spartina pectinata. \\ Scirpus robustus.

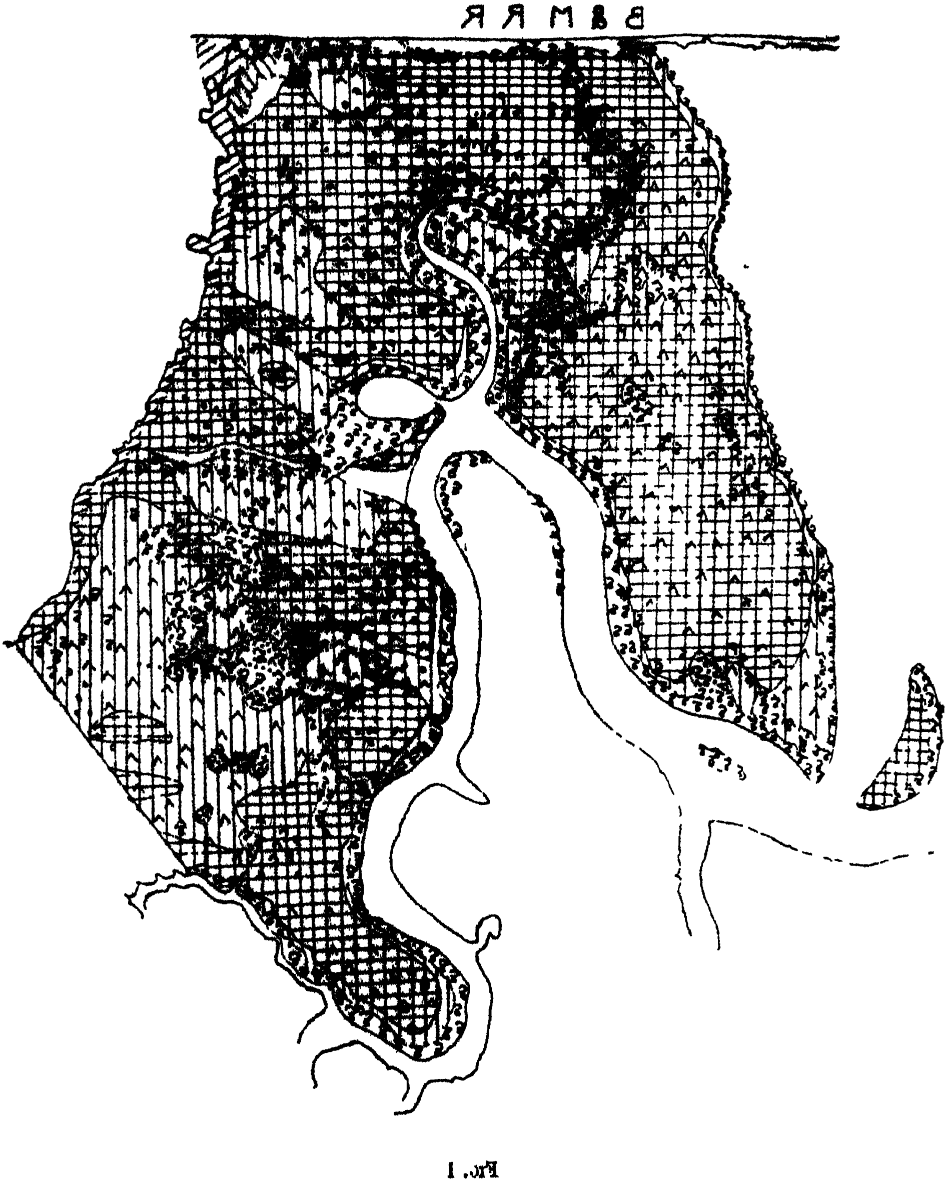

Fig. 1

The data are not as voluminous as those secured from the Norfolk marshes, but it is believed that their interpretation is substantially correct because it has been made in the light of the information obtained from Norfolk. It is also realized that the conclusions reached here may have to undergo some modification if data become available about the other factors.

Romney Marsh, between Saugus and Lynn, Mass., covers a large area, 4 miles long by ¾ mile wide, contains about 1000 acres (Mudge, 1858), and at present is still in a wild condition in spite of several roads across it (cf. Pl. 8). A large portion of this marsh was levelled by means of a "Y" level,[1] each position being selected carefully in relation to some particular vegetation community. The species and communities, both algal and phanerogamic, present at each site were carefully noted, and hence their ranges have been fairly accurately determined for this large marsh. The vegetation of one small area was mapped in detail for both the phanerogams and algae (Figs. 1, 2).

Physiography

The New England marshes may be said to extend from Maine to New Jersey where they have developed in front of a coast line formed of a glaciated hard-rock upland. They are characterized by being built of a marine peat, and this of course materially modifies some of the environmental factors when compared with the wholly silt marshes of Norfolk. This is one of the fundamental differences, and it must be borne in mind when making comparisons of the environment operating on these and the Scolt marshes. The peat is often of a considerable depth, 20 ft. or more, and this is to be correlated with the fact that they have developed, and perhaps still are developing, on a subsiding coastline. The evidence and arguments relating to this aspect of the problem have been dealt with more fully elsewhere (Chapman, 1938*c*) and hence will not be repeated here. The geology of many of these marshes has likewise been investigated very thoroughly and typical sections have been illustrated (Johnson, D. W. 1925; Shaler, 1886; Mudge, 1858), so that one is in a very good position to appreciate the edaphic conditions. The marine peat is to be found on top of a marine silt, on sand, or on the remains of a fresh-water bog in which stumps of *Pinus strobus* can still be found.

Most of the New England marshes are built up behind protecting barrier beaches which are often so built over (e.g. Revere Beach near Boston) that they are not easy to detect. There is little or no marine erosion because of the resistant character of the coastal rock, and so the marshes are composed principally of plant remains together with some silt from the rivers. All the larger marshes have fresh-water streams running through them, but they are said never to be flooded by fresh water. Islands of hard-rock upland are

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[1] The loan of this instrument was kindly arranged by Mr Bradford Washbourne of the Institute of Geographical Exploration, Harvard.

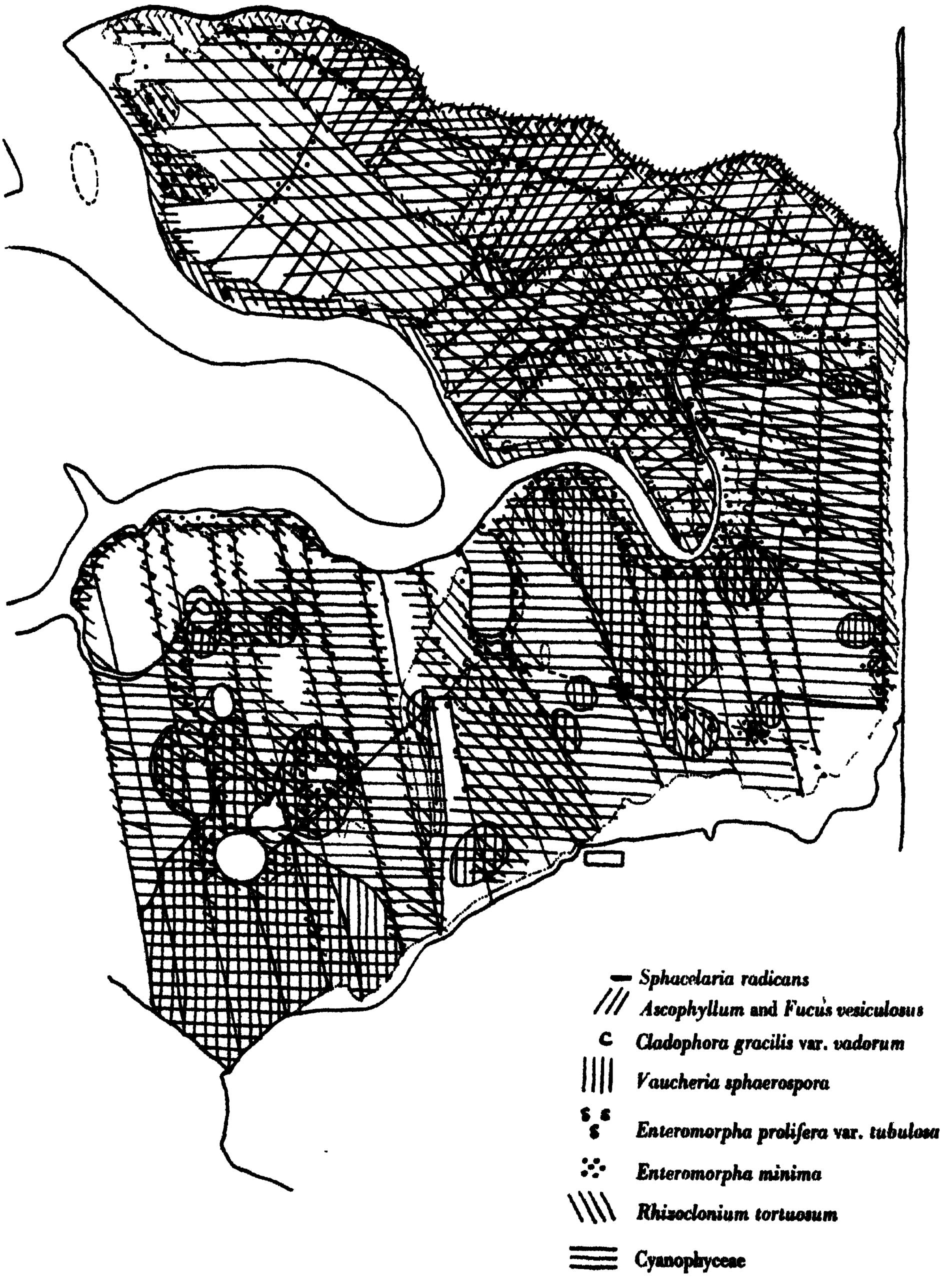
Sphacelaria radicans
Ascophyllum and Fucus vesiculosus
C Cladophora gracilis var. vadorum
Vaucheria sphaerospora
Enteromorpha prolifera var. tubulosa
Enteromorpha minima
Rhizoclonium tortuosum
Cyanophyceae

Fig. 2. Distribution of algal communities on part of Romney Marsh near Oak Island.

scattered through these large marshes, indicating that the marshes are not built upon a uniform surface.

The minor creeks on the marshes commence as runnels in the mud along which the water drains off, whilst scouring action by the tide prevents any vegetation from becoming established. With the advent of vegetation, deepening of the creeks takes place, principally through the deposition of successive layers of peat on the marsh. There is very little erosion comparable to that found in the English marine marshes, the compact nature of the peat resisting this process. We thus see that creek formation in England takes place primarily through erosion, whilst in America it is largely a building-up phenomenon. The protecting barrier beaches gradually move landward as a result of continual wave action and salt-marsh mud is occasionally exposed on the foreshore as a consequence. Such an exposure was seen in December 1935 near Bridgeport, Conn. (Pl. 9), and it is strictly comparable to similar phenomena to be seen at Scolt (Steers, 1934).

Scattered over the marshes are a number of pools or salt pans which, it has been stated (Nichols, 1920), are formed by the same means as those postulated by Yapp *et al.* (1917) for the Dovey marshes. My observations indicate, however, that only three of these methods appear to operate, whilst Smith (1907) has described another method, probably confined to these marshes, which is of great importance in that many of the pools appear to be formed in this way.

(*a*) Failure of the primary colonists to invade an area, which is subsequently kept bare by tidal scour. These pans can be observed on the very lowest marshes.

(*b*) The end sections of small creeks on the older marshes become dammed up by vegetation and so develop into pans. With the advent of the mosquito control ditches, which are scattered extensively over these marshes, one often finds that deep pans are developing where the ditches intersect; such pans, however, are purely artificial (the ditches appear as lines on Pl. 8).

(*c*) Large pans on older marshes become subdivided into a series of smaller pans through partial colonization.

(*d*) Depressed areas exist on the marshes, especially towards the upland and away from the creeks. Water collects in these depressions, the plants die off, probably due to the continual waterlogging, and rotting of the peat sets in so that large pools are ultimately formed. These pools have a very irregular outline with soft muddy sides, whereas pans of the previous types tend to have a sharply delineated outline (cf. Pl. 9).

With the digging of the ditches and the consequent drainage of the marsh and pans, rapid recolonization is taking place and in a few years there will be no pans left. Man's intervention will then have removed a natural feature of these marshes and replaced them by a series of artificial ditches.

Along the edges of the principal creeks and rivers a certain amount of undermining occurs and whole portions of the marsh to a width of 3–4 ft.

slip down and a secondary cliff is formed. This lowering of the marsh enables plants of an earlier phase to enter so that signs of a retrogressive succession can be observed.

The tides

The information was obtained by observing tidal movements on a graduated stake in one of the creeks of Romney Marsh which was levelled to the same datum as that employed for the vegetation, and correlating the movements of the tide on this stake with those obtained from the tide gauge in Boston Harbour. It then became possible to use the predicted Boston tides for 1935, as recorded by the tide-predicting machine on a chart[1], in order to extract information similar to that obtained for the Norfolk marshes (Chapman, 1938*a*). In addition, however, the tidal phenomena were calculated for the growing period so that the conditions on Romney Marsh could be compared with those at Cold Spring Harbour, Long Island, for which similar data was also available (Johnson & York, 1915). The salient features of the tides are summarized in Table 1.

Table 1

	Romney Marsh M.L.W. ft.	Long Island Marsh M.L.W. ft.	Scolt marshes M.L.W. ft.
Mean ht. max. spring tides	+10·48	+9·5	*c.* 16·7
Mean ht. min. neap tides	7·84	5·6	*c.* 11·7
Ht. of max. spring tide	11·50	—	*c.* 17·6
Ht. of min. neap tide	7·25	—	*c.* 10·3
Difference between spring and neap tides:			
Max.	3·84	—	7·08
Min.	1·33	—	1·99
Mean	2·60	—	4·87
Tidal range:			
Max.	13·26	10·8	*c.* 19·5
Min.	5·76	4·2	—
Mean	9·16	7·63	—

Table 2, which is an analysis of the tidal phenomena operating on Romney Marsh, has been built up from the predicted Boston tide curves for 1935. A study of this table indicates that Romney Marsh cannot be segregated into upper and lower marsh areas in the same way as the Scolt marshes (Chapman, 1938*a*), but Table 3 shows that the marsh on Long Island could be so divided at about +7·75 ft. M.L.W. It therefore remains to be seen how far this division into upper and lower marshes with different environmental conditions is general, and it would be highly desirable to have some more data for other marshes. An inspection of Table 2, however, will show that there is a very striking change in the maximum period of non-tidal exposure at about +9·4 ft. M.L.W. Immediately below this level the maximum non-tidal exposure is only 8 days, whilst immediately above it is 16. The long periods above 9·4 ft. M.L.W. occur during the late winter when the marsh is commonly

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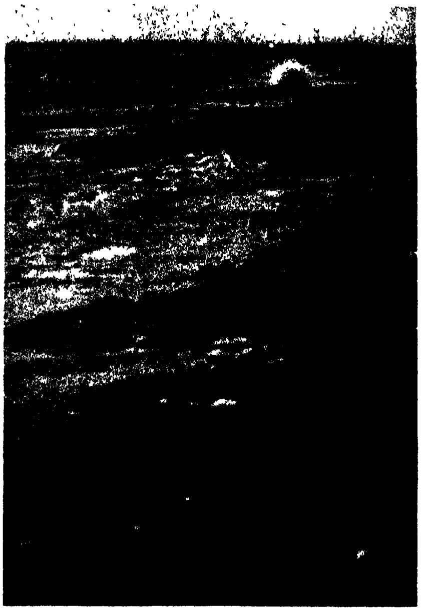
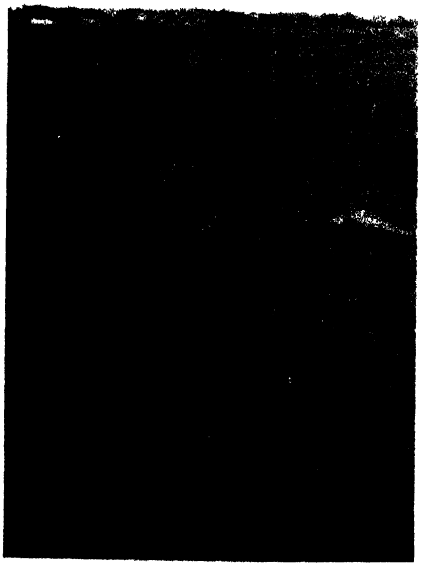
[1] The chart with the tracings was kindly provided by the U.S. Coast and Geodetic Survey.

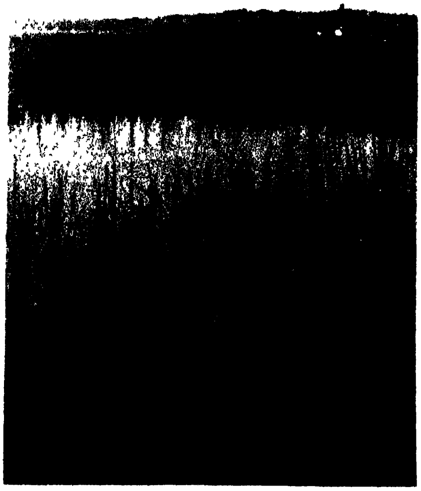


Phot. 1. Old marsh mud exposed on the foreshore at Stratford, Conn. The barrier beach has moved landwards over the marsh because of tidal attack.

Phot. 2. Air forced out of the marsh by the incoming tide and bubbling through the ice covering Cold Spring Harbour Marsh, Long Island.



Phot. 3. Salt pan formed by rotting away of peat: low tide.



Phot. 4. Salt pan formed by rotting away of peat: high tide.

frozen, so that the plants are subjected to extreme cold rather than to the extreme desiccation which is so characteristic of the upper marshes at Scolt which undergo their long periods during the summer months. Below 9·4 ft. the plants will not be subjected to intense cold for such a long period because although the water may freeze on top there is probably some tidal movement underneath. Whether this difference in non-tidal exposure would justify segregating the area into upper marsh above 9·4 ft. M.L.W. and lower marsh below that level is somewhat problematical. Until further information is available it would perhaps be premature to take this step.

Non-tidal exposure. Long periods of non-tidal exposure in summer may be extremely detrimental to plants, especially the algae, and hence it was important to ascertain the maximum periods tolerated by the different species. Diagrams were drawn in which the non-tidal exposures of seventeen phanerogamic and thirty-seven algal species were depicted for both their upper and lower limits on the marshes. It was found that they all agreed with one or other of the types illustrated in Fig. 3.

Hours of submergence per month. On Romney and Cold Spring Harbour marshes there is only one marsh phanerogam, *Spartina alterniflora*, with a lower limit below mean sea level (+2·81 ft. M.L.W. on Romney, +1·5 ft. M.L.W. at Cold Spring Harbour) whilst at Scolt only *Zostera nana* behaved similarly. *Zostera marina* var. *stenophylla* and *Ruppia maritima*, of course, exist wholly below mean sea level, but neither were frequent on the mud flats surrounding the Lynn and Boston marshes. Of the marsh algae studied (cf. Table 8) only two species on Romney Marsh had lower limits below mean sea level, *Oscillatoria nigroviridis* at +3·3 ft. and *Enteromorpha prolifera* f. *tubulosa* at +2·81 ft. At Cold Spring Harbour *Cladophora expansa*, *Lyngbya lutea*, *Rhizoclonium tortuosum*, *Spirulina tenuissima* and *Ulothrix flacca* were the only marsh algae with lower limits below mean sea level. It will be remembered that at Scolt none of the true marsh algae go below mean sea level although one or two have their lower limit near it.

Hours of submergence in daylight. None of the phanerogamic species on Romney Marsh (with the exception of *Spartina alterniflora*, *Zostera*, and *Ruppia*) descended below a level of +7·81 ft. M.L.W. where they would undergo, during the growing season, an average daily submergence in daylight of 4 hr. The marsh algae descended somewhat lower, but even they were limited to +6·72 ft. M.L.W. where they would be submerged for an average of 5 hr. in daylight each day throughout the year. The maximum submergence in daylight that any species could undergo is about 14 hr. per day, and it is important to note the small proportion of this period that can actually be tolerated by most of the species (cf. Table 2).

Table 2

Ft. above M.L.W. level	No. of submergences per annum	No. of submergences per growing season (May–Oct.)	Month of max. submergences	Max. non-tidal exposure	Month of max. non-tidal exposure	Av. hr. submerged per month (max. 733·7)	Av. hr. exposed per month (max. 733·7)	Av. hr. submerged per day per year	Av. hr. exposed per day per year
12·6	0	0	--	365	—	0	733·7	0	24
12·3	0	0	—	365	--	0	733·7	0	24
12·0	0	0	—	365	—	0	733·7	0	24
11·6	7	5	Oct.	287	Dec.–Jan.→ →Aug.	0·3	733·4	0·01	23·99
11·3	31	18	Sept.	75	May–July	1·95	731·05	0·06	23·94
11·0	59	33	Sept.	26	June–July	5·0	728	0·16	23·84
10·84	72	39	Sept.	24	Dec.–Jan., Jan., May, June–July, Nov., Dec.	6·7	727·0	0·22	23·78
10·74	82	43	Mar.–Apr., Aug.–Oct.	24	Jan., June–July, Nov., Dec.	8·3	725·4	0·27	23·73
10·60	101	55	Mar.–Apr., Aug.–Oct.	24	Jan.	11·4	722·3	0·37	23·63
10·42	115	62	Apr.–May, Sept.–Oct.	23	Jan.	14·5	719·3	0·47	23·53
10·3	144	81	May	22	Jan.	18·1	715·7	0·59	23·41
10·15	161	87	May	22	Jan.	22·0	711·7	0·7	23·3
10·0	198	105	May	20	Jan., Feb., Mar.	28·7	705·0	0·94	23·06
9·75	245	131	Apr., July	18	Jan., Mar.	45·7	688·0	1·5	22·5
9·5	318	168	May, Oct.	16	Feb.	53·4	680·3	1·7	22·3
9·3	372	193	May	8	Mar., Dec.	64·0	669·7	2·1	21·9
9·15	416	210	May, Aug., Sept.	7	Mar., Dec.	76·0	657·7	2·15	21·85
9·0	451	233	May, Aug.	6	Nov., Dec.	90·4	643·3	2·96	21·04
8·6	564	292	May, Oct.	3	Apr., Nov., Dec.	118·2	615·5	3·87	20·13
8·35	599	308	Oct.	1	Apr., May, Nov.	145·3	588·4	4·78	19·22
8·0	674	344	May, Oct.	0	—	175	558·7	5·7	18·3
7·81	683	350	May, Oct.	0	—	192·7	541·0	6·3	17·7
7·0	705	355	Months with 31 days	0	—	245·6	488·1	8·0	16
6·0	705	355	Do.	0	—	312·9	420·8	10·2	13·8
4·9	705	355	Do.	0	—	366·0	367·7	12·0	12
4·0	705	355	Do.	0	—	418·5	315·2	13·7	10·3
3·31	705	355	Do.	0	—	468	265·7	15·3	8·7
2·81	705	355	Do.	0	—	495·9	237·8	16·25	7·75
2·0	705	355	Do.	0	—	561·8	171·9	18·4	5·6
1·0	705	355	Do.	0	—	648·3	85·4	21·25	2·75
0·0	705	355	Do.	0	—	707·9	25·8	23·27	0·83

Table 2 (*continued*)

Month with max. hourly sub-mergence	Month with max. hourly exposure	Total hr. sub-merged per year	Total hr. sub-merged per growing season	Total hr. exposed per year	Total hr. exposed per growing season	Total hr. sub-merged in day-light per year	Total hr. sub-merged in day-light per growing season	Av. hr. sub-merged per day per year in daylight	Av. hr. sub-merged per day per growing season in daylight	Month of max. sub-mergence in day-light
—	Months with 31 days	0	0	8804	4464	0	0	0	0	—
—	Do.	0	0	8804	4464	0	0	0	0	—
—	Do.	0	0	8804	4464	0	0	0	0	—
Oct.	Jan., Mar. May, July, Aug., Dec.	3·9	3·6	8800·1	4460·4	1·9	3·65	0·015	0·02	Oct.
Oct.	Jan., Dec.	23·4	16	8780·6	4448	16·9	9·5	0·04	0·05	Oct.
Sept.	Jan.	60·5	38·3	8743·5	4425·7	38·8	17·1	0·1	0·08	Oct.
Sept.	Jan.	80·2	50·6	8723·8	4413·4	49	19·9	0·13	0·11	Oct.
Sept.	Jan.	99·4	61·7	8704·6	4402·3	61	23·8	0·18	0·13	Oct.
Sept.	Jan.	136·9	78·5	8667·1	4385·5	74·5	28·3	0·2	0·15	Oct.
Sept.	Jan.	174·2	99·8	8629·8	4364·2	94·7	34·4	0·25	0·18	Oct.
Sept.	Jan.	217·4	104·9	8586·6	4359·1	107·3	44·7	0·32	0·24	Oct.
May	Jan.	264·6	147·5	8539·4	4316·5	146·6	56·1	0·4	0·3	Dec.
May	Jan.	344·1	190·2	8459·9	4273·8	180·6	71·5	0·5	0·39	Dec.
May	Jan.	548·5	292·1	8255·5	4171·9	289·7	126·2	0·81	0·7	Dec.
May	Jan.	641·4	340·7	8162·6	4123·3	353·8	160·1	0·98	0·88	Dec.
May	Jan.	768·1	394·4	8035·9	4069·6	435·6	199·3	1·2	1·08	Dec.
May	Jan.	913·4	488·2	7890·6	3975·8	512·3	242·9	1·4	1·3	Nov.
May	Jan.	1084·6	578·3	7719·4	3885·7	617	303	1·7	1·66	Oct., Dec.
May	Jan.	1419	742·6	7385	3721·4	812·1	414·2	2·2	2·23	Oct., Nov.
May	Jan.	1743·2	907·9	7160·8	3556·1	1006·9	521·6	2·8	2·8	Oct.
May	Jan.	2100	1082·2	6704	3381·8	1221·3	650·5	3·38	3·5	May
May	Jan.	2312·8	1198·2	6491·2	3265·8	1363·2	743·8	3·77	4·0	June
May	Nov.	2947	1512·8	5854	2951·2	1746·8	942·7	4·83	5	May, June
Aug.	Nov.	3754·4	1967·6	5049·6	2496·4	2215·7	1229·8	6·0	6·6	Aug.
June	Jan.	4393·3	2257·6	4410·7	2206·4	2635·8	1452·3	7·4	7·9	July
Oct.	Jan.	5022	2569·8	3782	1894·2	2995·1	1675·4	8·35	9·1	July
Apr.	Jan.	5616·1	2834·5	3187·9	1629·5	3303·8	1847·1	9·18	10·0	July
Apr.	Jan.	5950·2	3042·6	2853·8	1421·4	3535·6	1980	9·84	10·75	July
July	Jan.	6741·7	3437·2	2062·3	1026·8	3949·3	2222	10·97	12·05	July
Oct.	Dec.	7779·7	3987·4	1024·3	476·6	4558·6	2592	12·6	14·02	July
July	Apr.	8494·6	4318·6	309·4	145·4	5062·7	2816	14·0	15·07	July

Table 3

Level (ft. above mean low water)	Ft. above M.S.L.	No. of submergences per season) (max. 355)	Periods of most frequent submergence	Max. consecutive period of submergences for any one month	Max. period of non-tidal exposure	Month with max. period of non-tidal exposure	Hours submerged per calendar month	Ratio: Submergence / Emergence	Average hours submerged in daylight	Ratio: Submergence / Emergence
				days	Upper					
8·75	5·15	18	May, Oct.	7 May	24	June–July	4·64	0·0063	0	0·0000
8·25	4·65	65	Sept., Oct.	15 Sept.	18	July	16·83	0·023	—	—
8·0	4·4	121	May, Aug.	23 May	16	July	30·36	0·043	—	—
					Lower					
7·5	3·9	200	July	38 July	8	May	47·2	0·054	—	—
7·25	3·65	229	July	44 July	6	May	67	—	—	—
7·0	3·4	284	June, July	54 June	5	Sept.–Oct.	97	0·152	0·48	0·0342
6·5	2·9	337	May, June, July	60 May, July	1	May, Oct.	161	0·280	—	—
6·25	2·65	343	May, June, July	60 May, July	¾	July, Aug., Sept., Oct.	177	0·316	—	—
6·0	2·4	351	May, July, Aug.	60 May, July, Aug.	¾	Sept., Oct.	202·8	0·380	—	—
5·0	1·4	355	May, July, Aug.	60 May, July, Aug.	Nil	—	375	0·596	—	—
4·0	0·4	355	May, July, Aug.	60 May, July, Aug.	Nil	—	339	0·853	—	—
3·0	−0·6	355	May, July, Aug.	60 May, July, Aug.	Nil	—	397·7	1·174	6·8	0·8830
−1·0	−4·6	355	May, July, Aug.	60 May, July, Aug.	Nil	—	732·8	198·0	—	—

Analysis of tidal phenomena at Cold Spring Harbour, L.I. (Johnson & York, 1915)

This table is based only on data from the months May–October. Mean sea-level is at 3·6 ft. M.L.W.

Water-table, aeration, and drainage

In section III of this series (Chapman, 1938*a*) the theoretical water-table relations that might be expected on an ideal set of marshes were discussed, and then an attempt was made to show how far these expectations were fulfilled. The New England marshes do not develop as a series with increasing height between shingle laterals as they do in Norfolk, and instead a gradual increase in height on a single marsh is to be noted as one goes landward. This type of marsh is represented diagrammatically in Fig. 4 where the highest portion of the marsh is near the upland and the lowest near the protecting barrier beach. Similar conditions are found in estuarine marshes, in which case the lowest portions will be those bordering the river. Apart from this fundamental difference in physiography, however, the general factors controlling access of

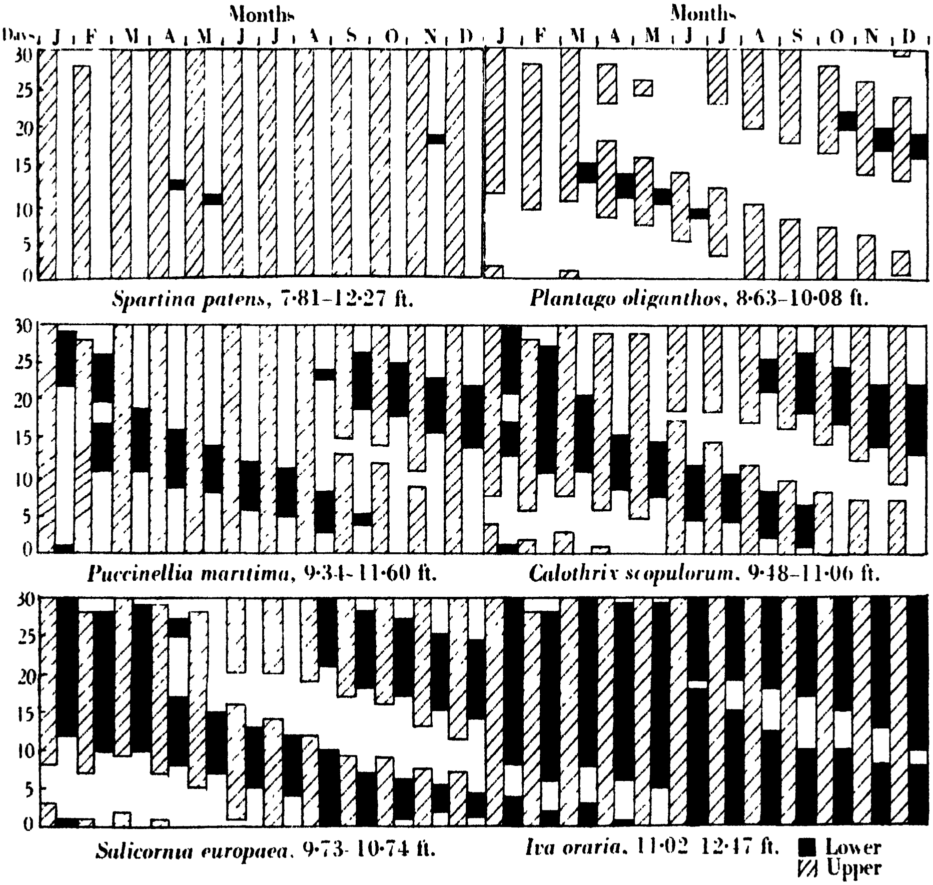


Fig. 3. Typical examples of the amount of non-tidal exposure undergone by plants at their upper and lower levels on Romney Salt Marsh.

water to a marsh and its subsequent removal are the same as those outlined in section III.

The movements of the marsh water-table cannot be understood unless the geological structure of the marsh is known. In the area studied in detail there was a depth of peat of 12 in., below which there was a peat in which much more silt was admixed. Measurements of the pore space of the upper peat gave values of 76–89%, but this high pore space is counterbalanced by the physical character of the peat which retains water tenaciously. So long as the peat is saturated, however, movement of the water may be expected to be relatively easy, but if the peat is not saturated then it will absorb water rapidly and there will be a consequent slowing down of any lateral water movement. Because of the evaporation that takes place during the inter-tidal periods it may be expected that the peat will dry out to some extent and hence will act as a sponge for at least part of the subsequent flood tide.

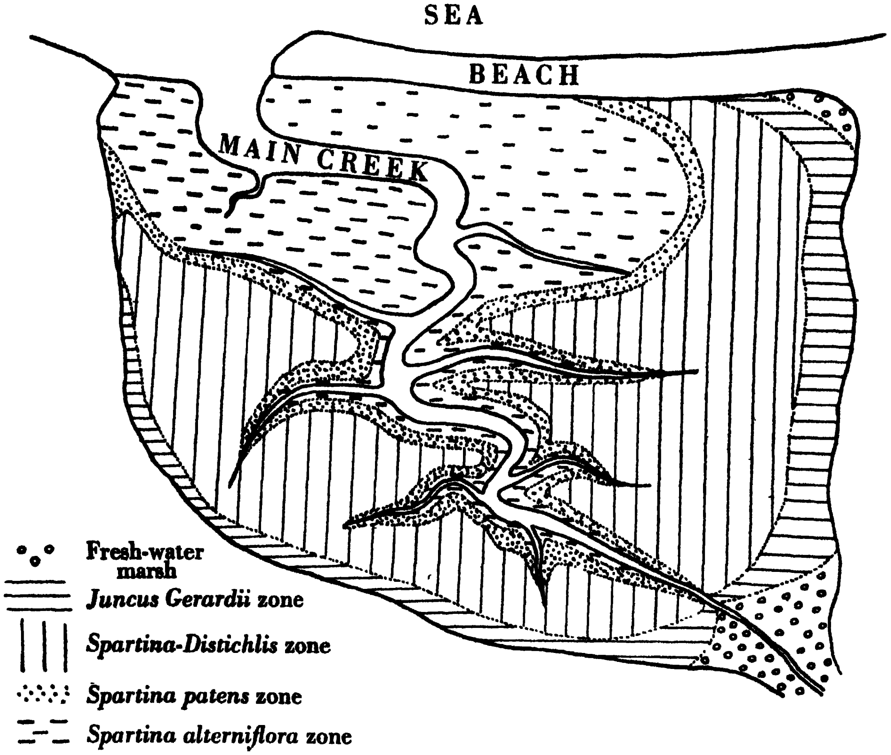


Fig. 4. Zonation with height on a typical New England marsh (diagrammatic).

When the superficial water drains off the marsh there is relatively little erosion at the sides of the creek banks and ditches because the peat is too firm to undergo erosion readily, and so breakdown of the banks is primarily due to undermining. Shingle laterals do not normally bound the sides of these marshes and hence all drainage must be either downward into the soil or else lateral into the creeks, although some seepage will take place directly into the sea through the barrier beaches when present. Until the advent of the drainage ditches the bulk of the water must have drained down slowly through the peat because the creek systems are not so prolific as those in Norfolk, but now that the marshes are intersected by the ditches it is probable that these form the channels for the removal of much of the water. The rate of drainage in different parts of the marsh will vary considerably, depending upon the depth of peat and the nature of the subsoil. On the Revere side of Romney Marsh, near the local airport, the peat lies on top of a stiff yellow clay so that downward drainage will be extremely slow, whilst in the Saugus part of the marsh the peat lies on a sand or sand-shingle substrate and here downward and lateral drainage will be rapid. It has been said (Smith, 1907) that deep ditches will drain an area extending laterally for a distance of 100 ft. from the ditch, but such observations as I have made suggest that this does not properly represent the situation. It may perhaps be true if there is a sand or shingle substrate, but it seems hardly possible if there is any depth of peat. Drainage, or lack of drainage, does not appear to determine the distribution of any species on the marsh although it does have a considerable effect upon the growth of plants. This is demonstrated clearly along the sites of ancient drainage ditches which can always be detected by the greater height of the vegetation.

Information about the movements of the water-table was secured by the use of tubes (the lower 6 in. of which were perforated) pushed into the marsh, and also by pits dug in the marsh. It was found impracticable to use the electrical recorders which were so successful on the English marshes (Chapman, 1938*a*), because the spongy peat retained so much liquid that the mere process of putting one of these recorders into the turf expressed sufficient water to give a record at once. The value of the pits was restricted, as in Norfolk, to non-flooding tides, and their records can only be used to confirm the more accurate ones obtained from the tubes (Figs. 5 and 6).

The data are not so extensive as those obtained from Norfolk, and furthermore, only a small portion of typical marsh was studied intensively. The records, however, have been interpreted in the light of the experience gained on the Norfolk marshes and hence the author feels justified in publishing them.

The results obtained showed that there was remarkably little movement of the water-table in the peat during a single spring or neap tide, probably due to the absorbent nature of the peat. However, they demonstrated that during a flooding tide the water-table did not usually rise completely to the surface, but remained 3 or 4 in. below (Fig. 7). This suggested the presence of an aerated layer extending from the surface to the water-table similar to that found in the Scolt marshes (Chapman, section III, 1938*a*). So far as seasonal movements are concerned the tidal cycles have a somewhat greater influence, as may be seen by an examination of Fig. 5 which also demonstrates that there is a definite downward gradient towards the creek and ditch. This gradient, however, does not extend to any great distance from either ditch

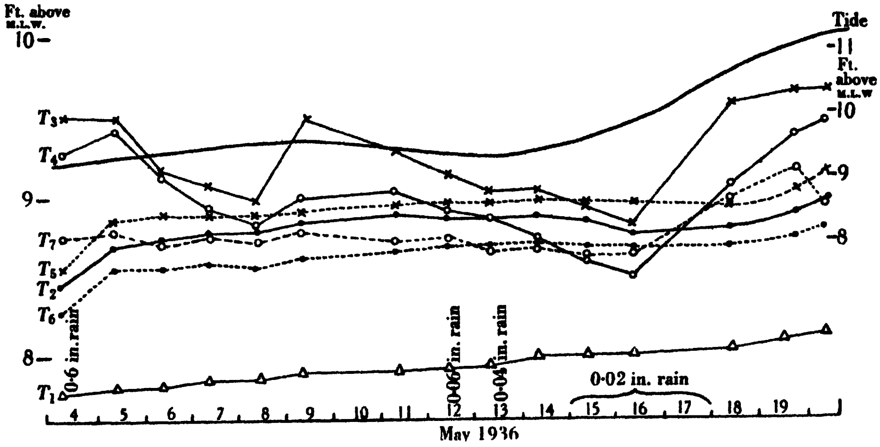


Fig. 5. Movements of the marsh water-table during a tidal cycle (tubes only).

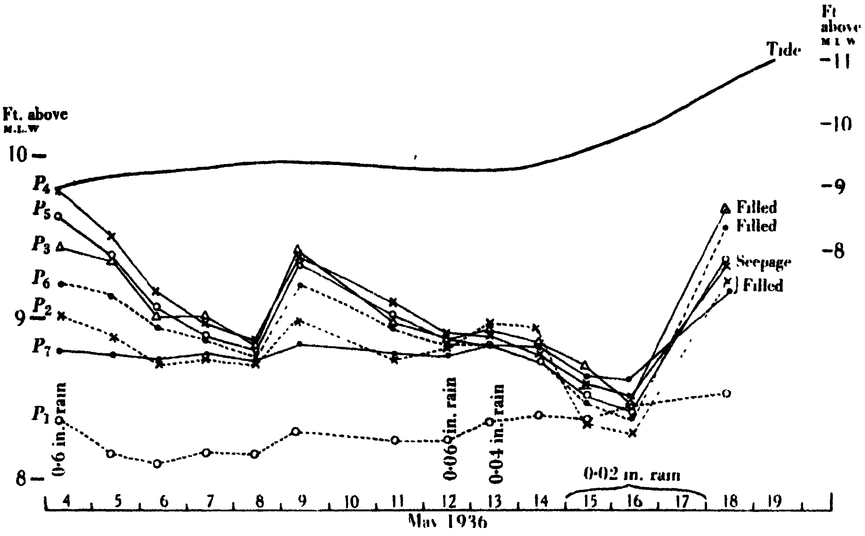


Fig. 6. Movements of the marsh water-table during a tidal cycle.

or creek. At no time was any evidence obtained which indicated that there were greater fluctuations in the water-table near creeks and ditches when compared with areas more remote. This suggests that drainage differences horizontally are very small, and certainly cannot account for the zone of *Spartina alterniflora* which is so conspicuous along the edges of the major creeks.

Aeration

The evidence which was obtained in order to confirm the existence of an aerated layer in the upper part of the marine peat is as follows:

(1) If, during a flooding tide, a stick is pushed into the peat and withdrawn, in most cases bubbles of gas emerge from the hole, whilst in some parts of the marsh the bubbles come out naturally through cracks in the soil (cf. Pl. 9).

(2) The evidence from the water-table movements in the tubes, as described above, indicated that the water rarely rose to within 3 in. of the surface during a flooding tide. The only exception to this was in a sunken recolonized area (Depression) surrounding a pan, where the peat was exceptionally loose and water movement very free. In such areas there is evidently no aerated layer, and as they are occupied by only a small number of species it may be this lack of aeration which prevents other species entering in to form the normal succession.

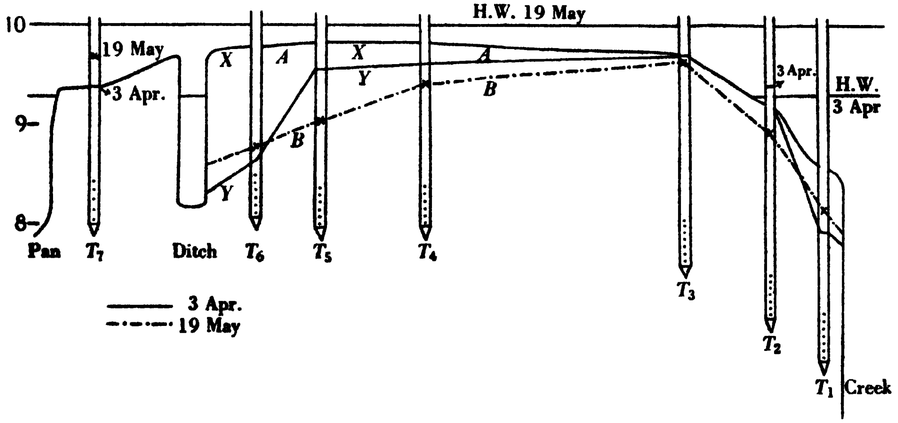


Fig. 7. Conditions in the soil of Romney Marsh at high water (3 Apr. and 19 May 1936), demonstrating the presence of an aerated layer. AB = aerated layer, 19 May; XY = aerated layer, 3 Apr.

(3) Manometers were sunk into the soil and observed during flooding tides. Those at levels of 6 in. and 9 in. invariably contained water in the cylinders at the conclusion of a tidal period, but those at 3 in. were free of such water; hence, the records of the latter really indicated a definite compression of the enclosed air (cf. Fig. 8).

(4) Some of the gas was extracted from the soil during a flooding tide, collected over a mixture of equal parts glycerine and saturated salt solution, and taken back to Harvard where the samples were analysed by Dr Dill of the Physiology Department in the School of Business Administration, to whom my thanks are due. Attention must be drawn to the values recorded from the *Spartina alterniflora* zone, and the composition of the gas here may

explain why other plants are absent from such areas. The low oxygen values cannot be regarded as lethal and it will be remembered that even lower values were recorded from gas obtained from the Scolt marshes (Chapman, 1938*a*).

Table 4

Site	CO_2 %	O_2 %	Residual gas %
Spartina alterniflora zone (1)	1·79	3·42	94·79
S. alterniflora zone (2)	3·23	8·28	88·49
S. patens zone	0·58	17·3	82·12
Distichlis spicata zone	1·17	17·3	81·53

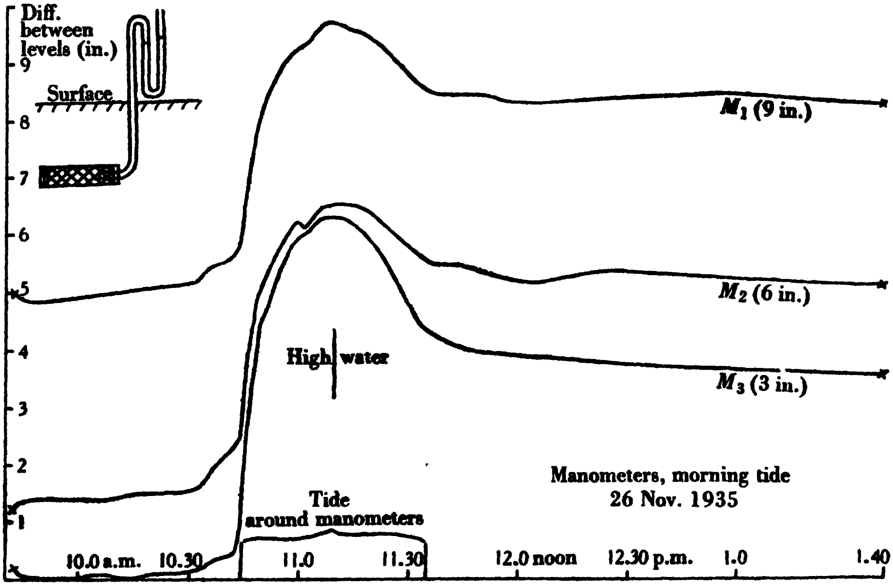


Fig. 8. Behaviour of manometers during a flooding tide.

(5) Penhallow (1908) has suggested that in the marsh there is a great accumulation of animal and plant remains and that when these decompose they give off a gas which may escape or be trapped.

So far as can be ascertained, the aerated layer is not wholly continuous. It may be absent close to ditches (due to infiltration of the tidal waters) and in the depressed recolonizing portions of pans (called, for convenience, "Depressions"). Local areas where it is absent in other parts of the marsh are to be explained by the presence of cracks in the soil surface, through which bubbles of air can be seen escaping at a flooding tide.

Salinity

This problem may be approached in the same way as it was for the Scolt marshes in section IV of this series (Chapman, 1939), namely, by considering what may be expected to happen in the various vegetation zones. Fig. 9

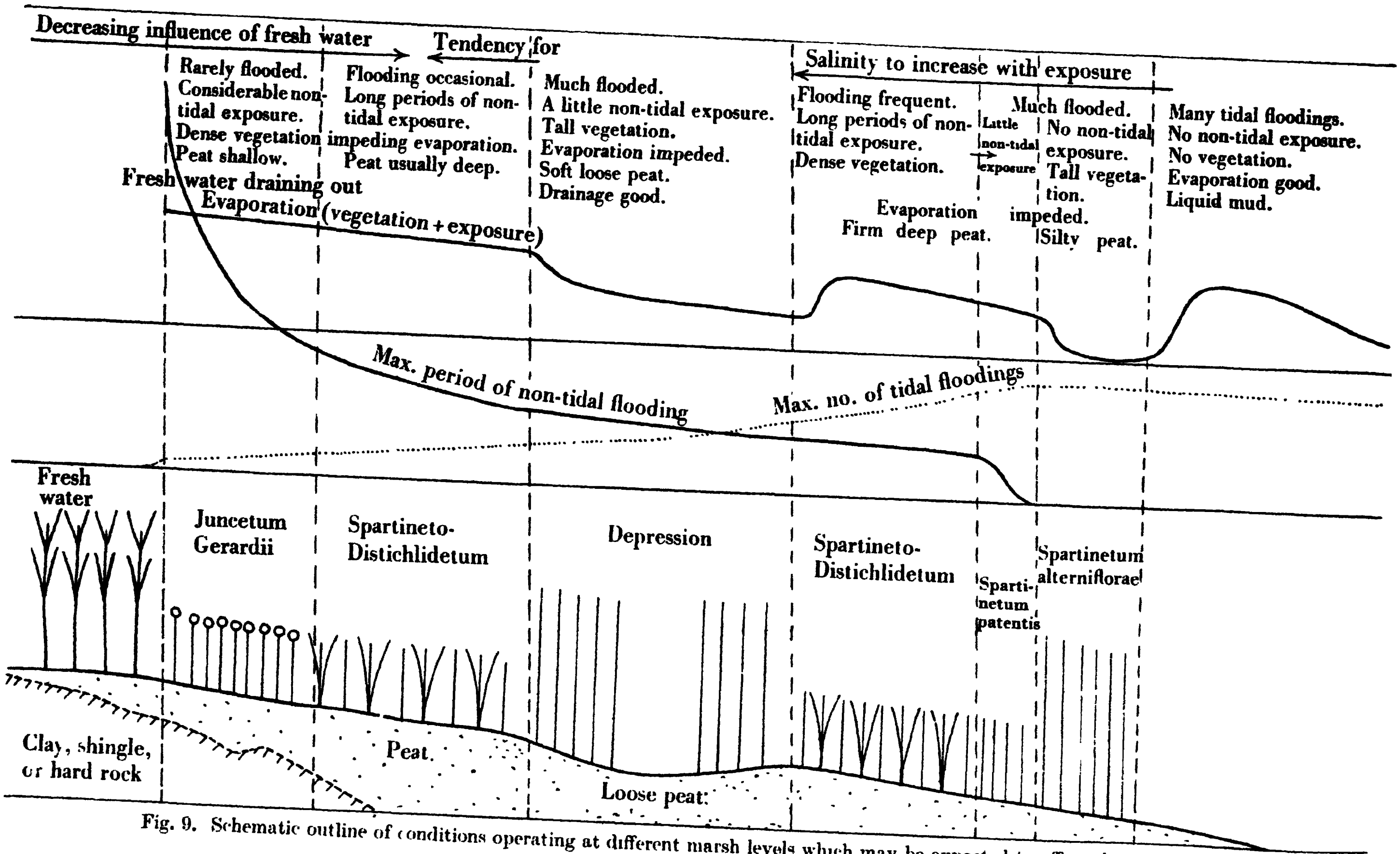


Fig. 9. Schematic outline of conditions operating at different marsh levels which may be expected to affect the soil salinity.

attempts to illustrate the principal vegetative and environmental features schematically and these may be considered separately in order to ascertain what may be expected to occur. The bare mud of creeks and low marsh is a soft liquid mud which is not subject to non-tidal exposure because it is covered at every tide. This continual flooding in itself will prevent the chloride content from rising very high and the retention of water in the mud will lower the values still more. This is a contrast to the more sandy mud of Scolt which drains much more readily and hence achieves a high salinity.

Spartinetum alterniflorae. This vegetation grows in a muddy peat in which there is some drainage, but the great height of the dominant species will prevent excessive evaporation, and, as there are no periods of non-tidal exposure, it may be expected that salinity will be low.

Spartinetum patentis. This narrow zone exists under much the same conditions as the previous and as the lower height of the vegetation is compensated for by its greater density there should be little difference in salinity.

Spartineto-Distichlidetum. The height of the vegetation is similar to that of the preceding zone, but as there are considerable periods of non-tidal exposure it might be expected that there will be some increase in the salinity. Towards the higher landward levels, however, the influence of fresh-water seeping down from the uplands and also coming in laterally from the main river may lower the rising salinity.

Juncetum Gerardii. Under normal circumstances it might be expected that the long periods of exposure and the relatively better drainage would result in a high salinity modified to some extent by the height of the vegetation. On the other hand the influence of fresh-water is much more marked on these marshes than on those of Scolt and this will counteract any increasing salinity.

Depressions. These are sufficiently low to undergo little or no non-tidal exposure and the peat is so loose that the water penetrates readily. The tall vegetation of *Spartina alterniflora* and its variety *pilosa* also tends to lower the evaporation so that a low salinity may be expected.

Compared with the Norfolk marshes, therefore, it will be seen that the tendency to increasing salinity is combated by the height and density of the vegetation together with the incidence of fresh-water. These marshes are much more uniform in appearance than those of Norfolk and hence one may expect to find the salinity varies less with change of level. So far as annual changes are concerned the highest values should be found in summer near the surface, but in winter all the marsh is frozen over so that there will be little fluctuation. At the time of the thaw in the spring, however, the great volume of water released will leach out the salt and the salinity should begin to decrease during the next few weeks, commencing at the surface.

A detailed study of the salinity changes in a small portion of Romney Marsh was undertaken between October 1935 and June 1936. Samples were collected from four separate plant communities about once a month throughout the period. Five sites were selected in each community and five samples were taken from the surface, 3 in., and 9 in. respectively. In the *Spartina alterniflora* zone the final samples were taken at 12 in. because of the greater length of the roots. The total chloride content of the samples was determined by the method described in section IV (Chapman, 1939). Filtration of the soil solution had to be carried out with a Buchner funnel as this was the only way in which all the water could be expressed from the peat. Fig. 10 shows the distribution of the vegetational zones from which the samples were regularly taken, but in addition to this series a number of selected sites on other marshes were also investigated throughout the period.

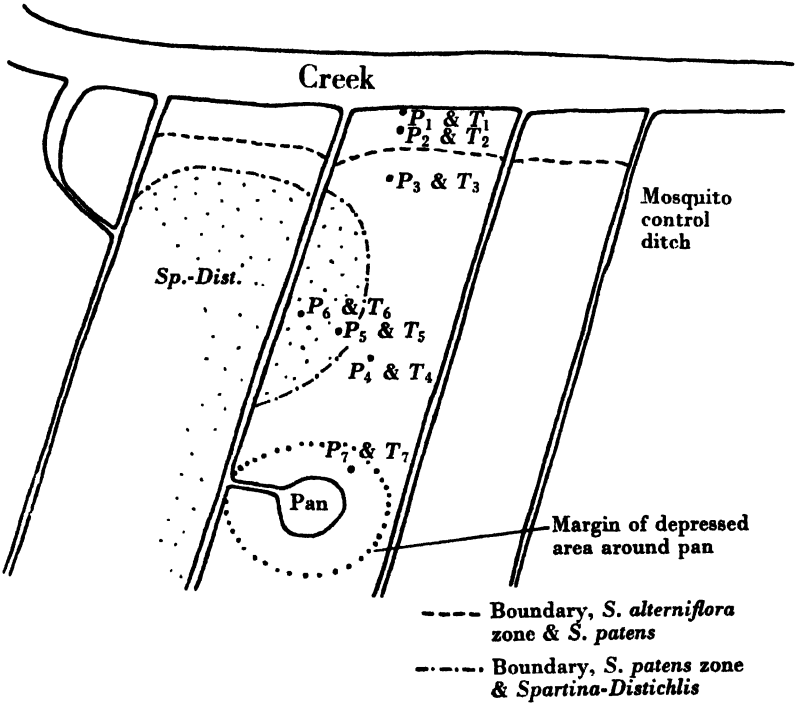


Fig. 10. Map of small portion of Romney Marsh near Oak Island showing distribution of pits and tubes and also the zones where the salinity investigation was primarily conducted.

Annual drift in salinity (Fig. 11). The principal features to which attention must be drawn are:

(i) the steady fall in the surface chloride content of all communities up to March, after which there is a rise;

(ii) the steady fall in chloride value of the 3 in. layer up to March or April, with a subsequent rise;

(iii) the fact that there is little or no progressive change in the chloride value of the 9 in. layer, which appears to be independent of season.

It will be seen that the chloride content in the surface and 3 in. layers usually attains to minimum values in successive months, the surface reaching the minimum first. *During May there is a reversal of the vertical gradient*, so that at the end of May there is a decreasing gradient with increasing depth. At the beginning of October, however, the chloride gradient increased with depth for most communities, *so that during the late summer months* (August and September) *there must have been another reversal of the vertical gradient. The yearly drift involves two changes in the vertical gradient, one just after the thaw in spring and one in the autumn when the rains commence.* The second reversal has been described by Steiner (1935), and, when allowance has been made for the difference in technique and mode of expressing the observations, his results show that it occurs in August or September.

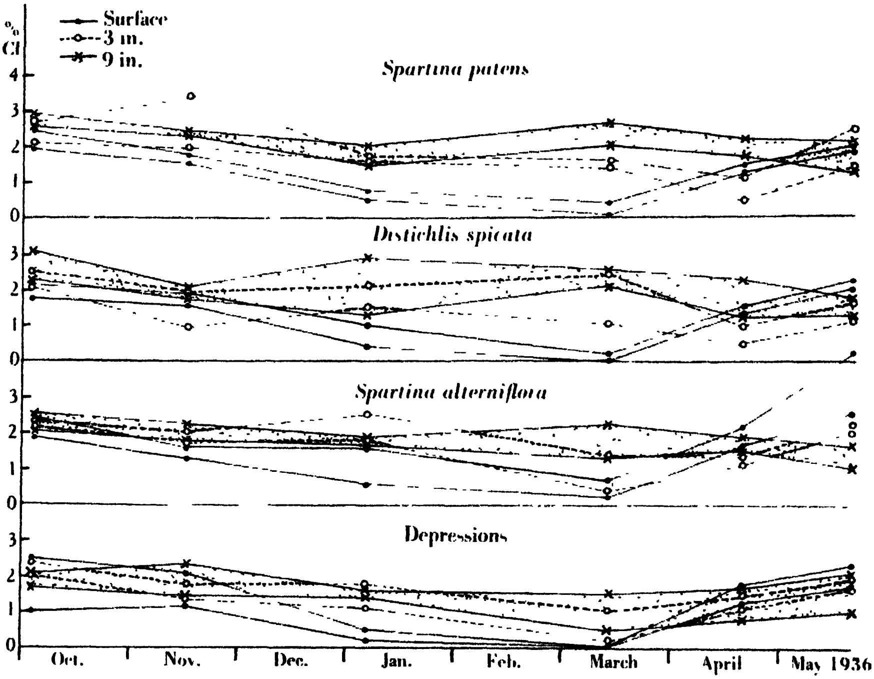


Fig. 11. Annual drift in chloride concentration.

It is also important to note that the surface chloride content in all communities attains its lowest values at the time of the year when seeds are germinating. This fact led me to believe that the seeds only germinate successfully because of these low values, which are all below 0·5% chloride, whilst Steiner (1935) has also commented on this feature in discussing colonization of pans by *Salicornia* spp. Germination experiments carried out in 1937 after 12 months' dormancy showed that germination was best in tap water or in a 1% chloride solution, whilst the seeds of some species, e.g. *Spergularia, Salicornia,* germinated better after they had been frozen.

Table 5. *Percentage germination 2 March–23 February* 1937 *after freezing*

	Salicornia mucronata		Spergularia marginata		Suaeda maritima		Plantago oliganthos	
Tap water	30	48	80	90	12	24	5	5
1% NaCl	28	50	100	95	6	10	0	0
2% NaCl	14	14	52	25	2	0	0	0
3% NaCl	2	8	32	0	0	0	0	0
Temp. ° C.	-10	-20	-10	-20	-10	-20	-10	-20

Horizontal variations (Figs. 12, 13). It will be seen that there is no general constant difference in salinity between the surface layers of the different communities. The values from the Depression around the pan were commonly lower than those from the other communities, whilst the 9 in. values from the Spartinetum patentis and Distichlidetum are conspicuously high. *The low values from the Depression can hardly be invoked to provide an explanation of the characteristic vegetation that is to be found in such places.* Steiner (1935) reports that the bare part of the pans may record very high values not only at the surface but down to a depth of 25 cm., but, unfortunately, he does not distinguish the type of pan with which he was dealing.

Vertical relations (Fig. 14). In the Spartinetum alterniflorae it will be noticed that in October there is practically no gradient with depth, in November and March there is a slight upward gradient with increasing depth, whilst in January there is a general *upward* gradient from the surface to the 12 in. layer. At the end of April the gradient shows signs of reversing and by the end of May slopes steeply downwards from the surface to the 3 in. layer and then rather less so to the 12 in. layer. In the Spartinetum patentis the gradient is upward from the surface to 9 in. in the period October to March, but then it shows signs of reversing in April and finally slopes very slightly down in May. In the Spartineto-Distichlidetum the curves show the same trend except that in November there was practically no gradient in either direction. In the Depressions there is a gradient in October from the surface *upwards* to the 3 in. layer with a slight fall from 3 in. and 9 in. From November to March there is an *upward* gradient from the surface to 9 in., whilst in May there is a *downward* gradient from the surface to 9 in. *There are, therefore, very distinct and definite seasonal changes in the vertical gradients, the evidence showing that from October to April the vertical gradient increases with depth, whilst from May to September the reverse is the case.* These general changes are represented in the series of small diagrams.

Chloride content in other communities (Fig. 15). Bare ground on the marshes can apparently be divided into two categories:

(*a*) Primary bare soil at the edges of creeks and in pans where there is a very soft mud. This is colonized by *Spartina alterniflora*, whilst the absence of *Salicornia herbacea* near creeks is probably to be associated with the instability of the surface mud (Wiehe, 1935) which prohibits *Salicornia* seedlings from becoming established because in the relatively undisturbed stable soil of the pans *Salicornia* grows vigorously.

(*b*) Secondary bare soil on the marsh proper where there is a very distinct peat. In such places the plants have died: (i) because of a deposit of trash (stems and leaves of *Spartina alterniflora*), or (ii) through burning (certain parts which already have a feeble vegetation are bared by heavy burning).

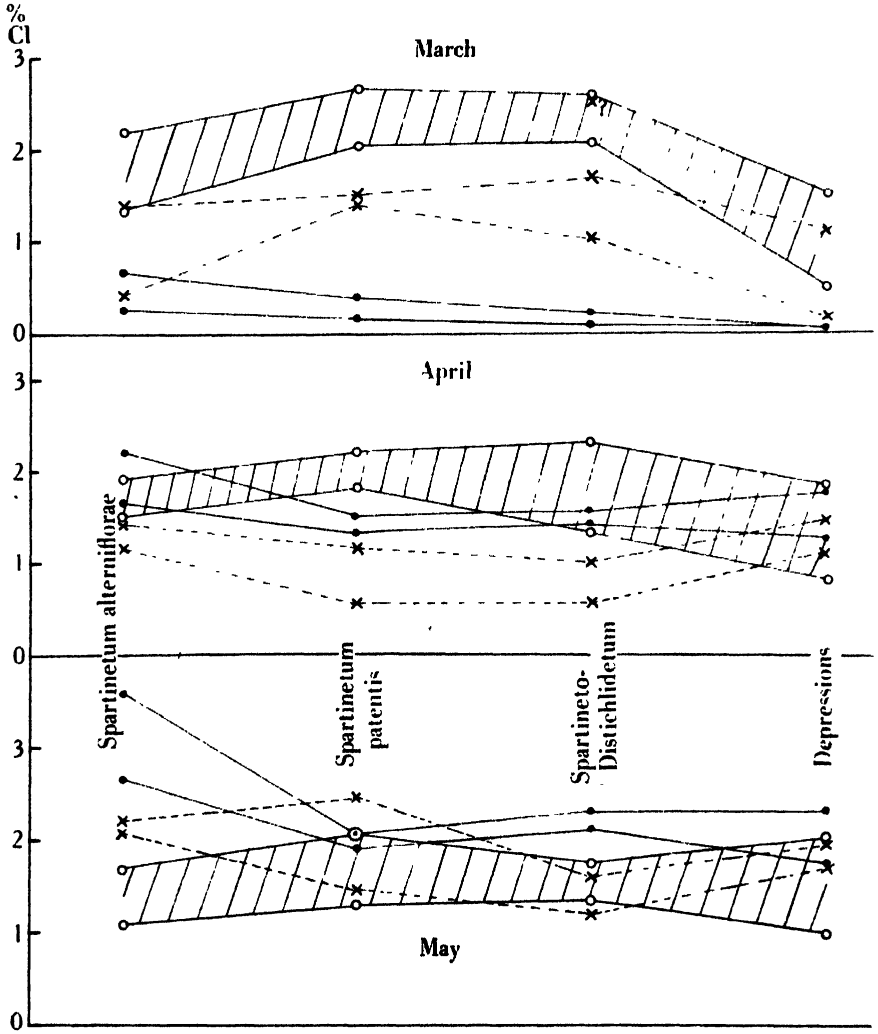


Fig. 12. Horizontal variations in chloride content.

The primary bare liquid soil of the river beds and in many of the pans has a low chloride value, so that it cannot be this factor which prevents plant colonization. It is more probably the mechanical difficulty of seedling establishment (cf. Wiehe, 1935), or perhaps the submergence factor. Secondary bare soil usually exhibits very high chloride values, especially in the 3 in. layer, and it may be suggested that the difference in the salinity content of primary and secondary bare soil may be correlated with the soft mud of the one and the firm peat of the other.

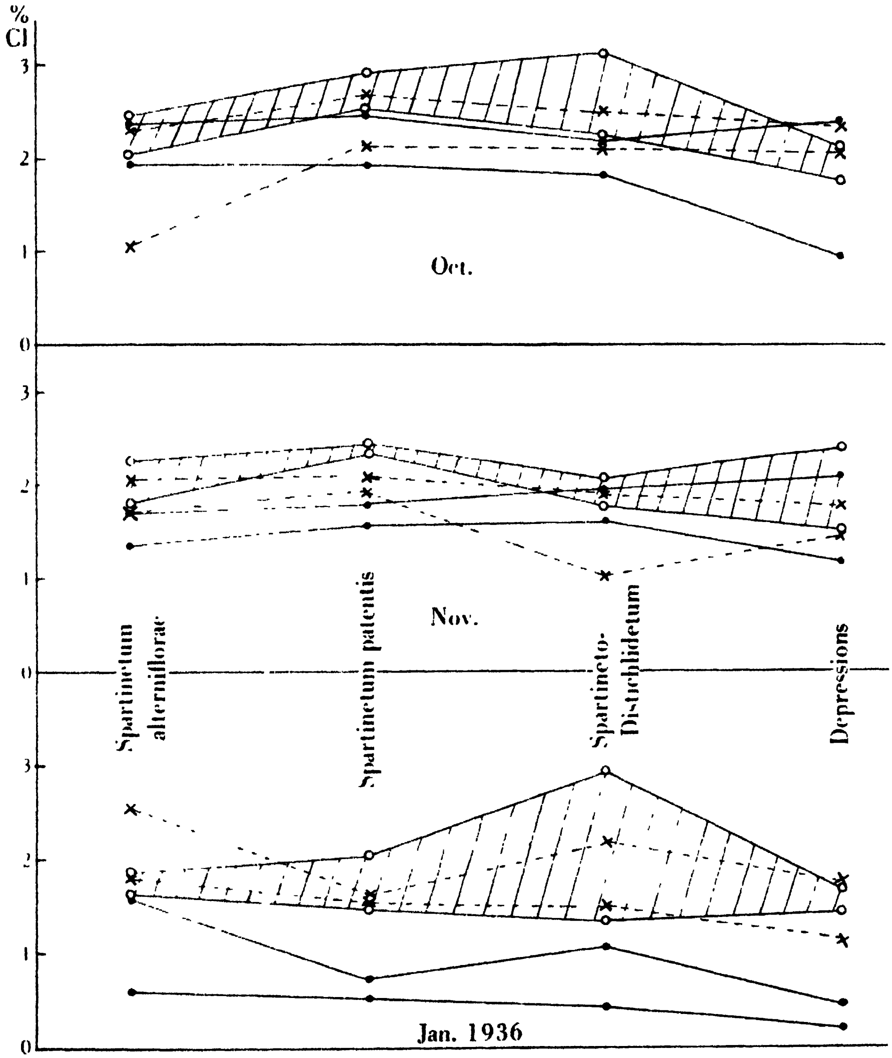


Fig. 13. Horizontal variations in chloride content.

In Diagram 15 it will be seen that the surface chloride values rise from the bare mud of the creek bed to the *Spartina alterniflora* zone, but thereafter fall gradually with increasing height of the marsh above sea level. Slightly higher values than usual are found in the pan Depressions and the Scirpetum,

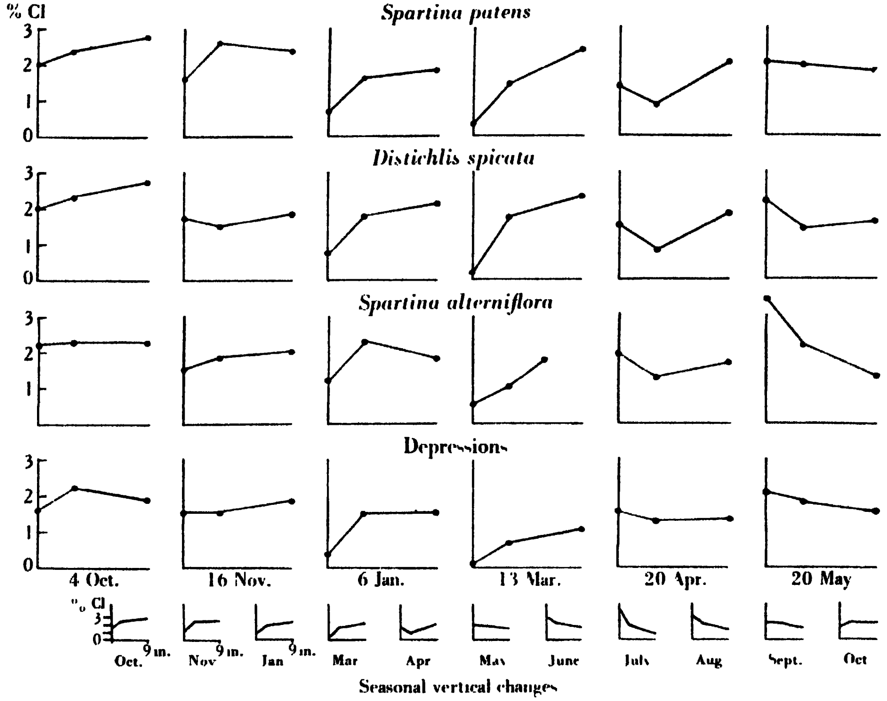


Fig. 14. Relation of average chloride content to depth of soil.

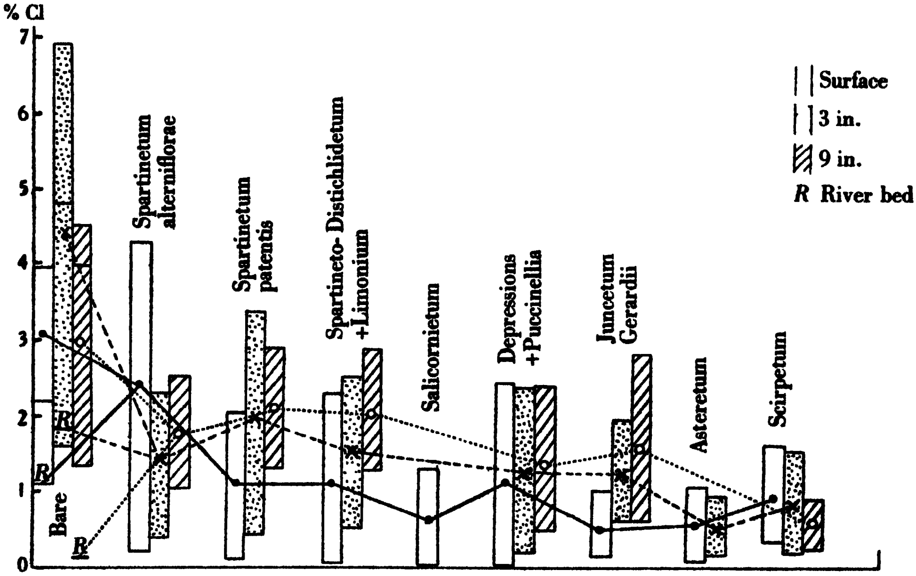


Fig. 15. Chloride ranges from different communities on the New England salt marshes.

although it is doubtful whether they are significant, but an important feature is the relatively low values that are recorded from *Salicornia* habitats. A similar phenomenon has been observed on English marshes (section IV, Chapman, 1939) and it is suggested that *Salicornia* has the power of removing chlorides from the soil in sufficient quantity to affect the salinity content of the soil itself. In the 3 in. layer there is a slight downward gradient from the creek mud to the *Spartina alterniflora* zone, but this is followed by a rise to the *Spartina patens* zone with a subsequent steady fall with increasing height of the ground. The value from the Asteretum is exceptionally low and it will be suggested in another communication that the distribution of *Aster* is associated with these low chloride values. In the 9 in. layer there is an increasing gradient from the creeks to the salt hay grass zones followed by a decreasing gradient with further rise of level.

The bulk of the roots of the different species will be in the 3 in. or the 9 in. layers, and the chloride content at these depths exhibits relatively little variation compared with that of the surface. On the other hand, during the winter months the chloride content in these layers may be considerably greater than that of the surface layer because they probably do not freeze. The relative constancy in these layers may permit plants to exist on the marshes because the osmotic pressure of the roots is not required to fluctuate violently in order to meet similar fluctuations in the concentration of the soil solution. On the other hand, the shallow roots of *Salicornia* spp. and *Puccinellia maritima* must be able to adjust themselves to relatively large changes in chloride concentration during the course of a year.

Moisture

The results of the moisture determinations indicated that this factor did not determine the plant distribution on the marsh, the values for the different levels showing very little fluctuation throughout the period. The surface layers of the Spartinetum patentis, Spartineto-Distichlidetum and the Depressions around the pans rose to a maximum value in January just before the ground became frozen. This is probably to be correlated with decreased evaporation. It is probable that the surface moisture would reach a minimum during July and August when evaporation is at its height, but unfortunately the author was not present at this time of the year.

VII. THE VEGETATION OF THE AMERICAN MARSHES

The phanerogams

It is not proposed to describe the phanerogamic vegetation in detail, as earlier accounts (Harshberger, 1911; Conard, 1935; Nichols, 1920; Smith, 1907; Townsend, 1913) have done this adequately. The principal feature is the overwhelming dominance of the grasses, and yet in the autumn of 1935 very few viable seeds were set, but as this phenomenon has been observed before (Townsend, 1913) it is clear that the bulk of the grass colonization is secured slowly but surely by rhizomes. Certain species are more abundant on the southern New England marshes than they are on those around Boston (e.g. *Elymus virginicus* var. *halophilus*, *Gerardia maritima*, *Pluchea camphorata*, and *Lilaeopsis chinensis*).[1]

The phanerogamic consocies which could be recognized on Romney Marsh are as follows:

Table 6. *Romney Marsh, phanerogamic consocies and levels*

Consocies	Limits Upper ft. M.L.W.	 Lower ft. M.L.W.	Vertical range ft.
Spartinetum alterniflorae	10·74	3·31	7·43
Spartinetum patentis	11·06	8·26	3·80
Spartineto-Distichlidetum	11·06	9·14	1·92
Juncetum Gerardii	11·69	9·74	1·95
Spartinetum pectinatum	11·97	10·42	1·55
Scirpetum	?	10·12	—

These figures show conclusively that on this marsh (and it appears to be generally true of the northern marshes) *Spartina patens* forms a zone between the Spartinetum alterniflorae and the Spartineto-Distichlidetum.

The following socies can also be recognized, two of which have not been described previously:

Table 7. *Phanerogamic socies of Romney Marsh and the levels*

Socies	Limits Upper ft. M.L.W.	 Lower ft. M.L.W.	Vertical range ft.
Salicornietum	10·06	9·81	0·25
Plantagineto-Limonietum	10·08	8·63	1·45
Spartineto-Puccinellietum	10·84	10·21	0·63
Suaedetum maritimae	11·05	8·63	2·42
Asteretum subulatum	12·60	10·62	1·98

The Plantagineto-Limonietum occupies small areas in the Spartinetum patentis or Spartineto-Distichlidetum, and although these areas are often only a few feet across nevertheless *Limonium trichogonum* and *Plantago oliganthos* are the dominant species, although they may be accompanied by plants of *Triglochin maritimum*, *Distichlis spicata*, and *Spartina patens*. In the Spartineto-Puccinellietum the dominant species are *Puccinellia maritima* and *Spartina alterniflora* (large and dwarf forms (Steiner, 1935) and also var. *pilosa*), whilst the associated species are *Limonium trichogonum*, *Salicornia herbacea*, and *Suaeda maritima*. Table 8 is a summary of the vertical ranges of the principal phanerogamic and algal species that can be found on Romney Marsh.

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[1] The authority used for the phanerogamic species, unless otherwise indicated, is Fernald, Robinson, and Gray's handbook (1908).

Table 8

Species	Max. level ft. M.L.W.	Min. level ft. M.L.W.	Range ft.
Phanerogams:			
Scirpus robustus	?	10·12	—
Aster subulatus	12·6	10·62	1·98
Iva frutescens var. oraria	12·47	11·02	1·45
Solidago sempervirens	12·41	10·77	1·64
Atriplex hastata	12·08	? 10·6	1·48
Spartina pectinata	11·97	10·42	1·55
Juncus Gerardii	11·69	9·74	1·95
Puccinellia maritima	11·60	9·31	2·29
Triglochin maritimum	10·73	9·52	1·21
Salicornia herbacea	10·74	9·73	1·01
Spartina patens	12·27	7·81	4·46
Limonium trichogonum	11·93	8·35	3·58
Distichlis spicata	11·27	8·98	2·29
Suaeda maritima	11·27	8·63	2·64
Spartina alterniflora var. pilosa	10·84	8·12	2·72
S. alterniflora	10·74	2·81	7·93
Plantago oliganthos	10·08	8·63	1·45
Algae:			
Phaeococcus adnatus	11·93	10·08	1·85
Endoderma perforans	11·69	9·81	1·88
Gloeocapsa crepidinum	11·34	9·51	1·83
Calothrix scopulorum	11·06	9·48	1·58
Nodularia Harveyana	10·84	9·80	1·04
Ulothrix flacca	12·41	8·44	3·97
Microcoleus tenerrimus	11·93	8·12	3·81
M. chthonoplastes	11·93	6·72	5·21
Phormidium corium	11·93	8·44	3·49
P. angustissimum	11·69	9·05	2·64
P. papyraceum	11·34	6·72	4·62
Ulothrix implexa	11·68	9·09	2·59
U. subflaccida	11·23	8·35	2·88
Lyngbya lutea	11·12	9·29	1·83
Oscillatoria sancta	11·12	8·12	3·00
O. corallinae	11·06	6·72	4·34
Rhizoclonium tortuosum	11·12	6·72	4·40
Phormidium tenue	11·11	6·72	4·39
P. autumnale	11·05	9·23	1·82
Urospora isogona	10·84	9·23	1·61
Lyngbya semiplena	11·05	8·63	2·42
L. confervoides	11·02	6·72	3·30
L. aesutarii	10·84	8·35	2·49
Spirulina subsalsa	10·84	6·72	4·12
Chroococcus turgidus	10·74	9·09	1·65
Vaucheria Thuretii	10·74	8·44	2·30
V. sphaerospora	10·63	9·09	1·54
Oscillatoria margaritifera	10·54	9·20	1·34
O. nigroviridis	10·47	3·31	7·16
Rhizoclonium implexum	11·11	8·35	2·76
Lyngbya majuscula	10·45	9·36	1·09
Cladophora gracilis	10·35	8·63	1·72
Spirulina labyrinthiformis	10·35	8·44	1·91
Calothrix confervicola	10·35	8·44	1·91
Ent. prolifera f. tubulosa	10·06	2·81	7·25
Ent. minima	10·05	6·72	3·33

The algae

So far as can be ascertained there are no detailed studies of the algal communities of the New England marshes. It is to be regretted that so short a time was spent on these marshes but, nevertheless, a number of definite algal communities have been recognized, some of which are very similar to those described from England (Carter, 1932, 1933; Chapman, 1937, 1939). Owing to the height and density of the vegetation there are fewer algal species and the communities are not so extensive as those on the more open Scolt marshes.

Over nearly all the marshes there is a general Chlorophyceae association (range +8·35–10·84 ft. M.L.W.) which can be divided into a Rhizoclonietum and a Cladophoreto-Enteromorphetum.

General Chlorophyceae association. 8·35–10·84 ft. M.L.W.

(*a*) *Rhizoclonium*, 8·35–10·84 ft. M.L.W.

Rhizoclonium tortuosum[1]	d.[2]	Urospora isogona	l.r.
R. implexum	r.–o.	Cladophora expansa	l.r.
Ulothrix flacca	l., r.–f.	C. gracilis var. vadorum	l.r.
U. subflaccida	l.r.–o.	Monostroma latissimum	l.r.
Enteromorpha clathrata	l.r.	Endoderma perforans	l.r.
E. prolifera f. tubulosa	l.o.	Phaeococcus adnatus	l.f.
E. torta	l.r.–l.o.	Oscillatoria nigroviridis	r.–o.
E. clathrata f. prostrata	l.o.	O. margaritifera	r., l.
Phormidium corium	o.–f.	O. corallinae	r.–f.
P. angustissimum	f.	O. sancta	r.–o.
P. tenue	r.–o.	O. formosa	l.r.
P. papyraceum	r.–f.	Spirulina labyrinthiformis	l.f.
Microcoleus chthonoplastes	o.–a.	S. subsalsa	o.–f.
M. tenerrimus	r.–l.o.	Nodularia Harveyana	l.–o.
Lyngbya confervoides	o.–f.	Calothrix confervicola	r., l.
L. lutea	o.–f.	C. Contarenii	l.r.
L. semiplena	o.–f.	Chroococcus turgidus var. maximus	l.r.
L. aestuarii	r.–f.		
L. majuscula	l.r.–l.o.	C. minutus	l.r.
Vaucheria sphaerospora	l., o.–f.	Aphanocapsa marina[3]	l.o.
V. Thuretii	l.r.–l.f.		

This community, characterized by the overwhelming dominance of *Rhizoclonium tortuosum*, is to be found in all the phanerogamic communities, but it is not so common in the Spartinetum alterniflorae and Juncetum Gerardii although it is frequently present along the edges of ditches. The associated species may be few or numerous, depending on local conditions.

(*b*) Cladophoreto-Enteromorphetum, +8·63–10·35 ft. M.L.W.

Cladophora expansa	f.–a.	Phormidium autumnale	l.o.
C. gracilis var. vadorum	l.a.	P. corium	l.a.–o.
C. fracta	l.a.	P. angustissimum	l.r.
Rhizoclonium implexum	o.–f.	Nodularia Harveyana	r.
R. tortuosum	o.–f.	Merismopedia glauca	l.r.
Ulothrix implexa	l.r.	Aphanocapsa marina	r.
U. flacca	f.–l.r.	Enteromorpha crinita	f.–a.
U. subflaccida	r.–o.	E. clathrata f. prostrata	f.–a.
Microcoleus chthonoplastes	r.–f.	E. prolifera f. tubulosa	l.a.
M. tenerrimus	o.	E. minima	l.–l.f.
Phormidium tenue	r.–f.	E. torta	l.r.–l.o.

[1] A note concerning the confusion of this species with *Chaetomorpha tortuosa* has appeared in *Rhodora* (Chapman, 1938*b*).

[2] d. = dominant, a. = abundant, f. = frequent, o. = occasional, r. = rare, l. = local.

[3] The authorities for the algal species are Newton (1931), Farlow (1881), and Geitler (1932).

Enteromorpha usneoides	l.a.	Spirulina subsalsa	o.–r.
Vaucheria Thuretii	o.–f.	S. labyrinthiformis	l.r.
Urospora isogona	l.o.	Oscillatoria sancta	l.f.
Lyngbya confervoides	r.–l.f.	O. nigroviridis	r. f.
L. aestuarii	o.–f.	Calothrix scopulorum	o.
L. semiplena	l.f.	Chaetomorpha tortuosa	o.
Calothrix confervicola	o.–f.		

This is largely confined to the pan Depressions but it may also occur in the Spartinetum alterniflorae zone along the creeks. It occupies very damp areas and is always associated with a stand of *Spartina alterniflora.* It is characterized by the dominance of species of either *Cladophora* or *Enteromorpha* or of both.

Vaucherietum. +9·31 10·38 ft. M.L.W.

Vaucheria sphaerospora	d.	Ulothrix implexa	r.
V. Thuretii	l.d.	U. subflaccida	l.r.
Rhizoclonium tortuosum	o.-f.	Lyngbya confervoides	o.–f.
R. riparium	l.r.	L. lutea	l.f.
Phormidium autumnale	o.–f.	L. aestuarii	r.–f.
P. corium	o.–f.	L. semiplena	r. o.
P. tenue	o.- f.	Oscillatoria margaritifera	o.
P. papyraceum	o.–f.	O. nigroviridis	o.
P. angustissimum	l.o.	O. corallinae	r. f.
Spirulina subsalsa	r.–f.	O. laetevirens	r.
Microcoleus chthonoplastes	o.–f.	O. subuliformis	r.
M. tenerrimus	o. f.	Gloeocapsa crepidinum	r.
Nodularia Harveyana	r.–l.o.		

This community is common in the Spartinetum patentis and Spartineto-Distichlidetum where it usually occurs in rather open areas, especially where the grass has been burnt the preceding year. Under these conditions there is more light penetrating to the soil and *Vaucheria sphaerospora* thrives. *V. Thuretii* occurs only locally, usually on the mud banks of small creeks in the older portions of the marsh.

General Cyanophyceae association. +6·72 -11·93 ft. M.L.W.

Phormidium corium	f. -a.	Oscillatoria margaritifera	r.–a.
P. angustissimum	f.- a.	O. sancta	f.- a.
P. papyraceum	l.f. a.	O. nigroviridis	f.
P. tenue	o.– a.	O. corallinae	o.
P. autumnale	o.- a.	O. laetevirens	r.
P. foveolarum	l.o.	Chroococcus turgidus	o.- r.
Lyngbya confervoides	f.	Spirulina subsalsa	f.
L. aestuarii	o., l.f.,	S. labyrinthiformis	l.o.
L. aestuarii var. spectabilis	l.r.	Microcoleus chthonoplastes	f. -l.a.
L. lutea	o.–f.	M. tenerrimus	o.
L. semiplena	l.–o.	Aphanothece pallida	o.
L. majuscula	l.r.–l.o.	Anabaena variabilis	l.r.
Calothrix scopulorum	l.f.- l.a.	Gloeocapsa crepidinum	r. l o.
Nodularia Harveyana	o.	Nostoc Linckia	r.
Vaucheria sphaerospora	o.	Merismopedia glauca	l.r.
Rhizoclonium tortuosum	o.	Urospora isogona	l.o.
R. implexum	o.	Ulothrix implexa	l.o.
Endoderma perforans	o.	U. subflaccida	l.r.
Enteromorpha clathrata f. prostrata	l.	Phaeococcus adnatus	l.r.–l.o.

This community is abundant over all the marshes being especially well developed in the damper areas, e.g. in the Spartinetum alterniflorae.

Vernal Ulothrix community. +9·31–11·68 ft. M.L.W.

Ulothrix implexa	a.	Rhizoclonium implexum
U. flacca	a.	R. tortuosum
U. subflaccida	a.	Endoderma perforans
Monostroma latissimum		Oscillatoria nigroviridis
Phormidium papyraceum		O. sancta
P. tenue		Spirulina subsalsa
P. foveolarum		Microcoleus chthonoplastes
P. corium		Lyngbya confervoides
Lyngbya semiplena		L. lutea

The community is only to be found in the spring and early summer during the few months after the thaw of the ice, when it is very abundant on the vertical walls of the ditches and also on stems of *Spartina patens* and *Spartina alterniflora*.

Gelatinous Cyanophyceae. +11·09 11·34 ft. M.L.W.

Gloeocapsa crepidinum	a.	Phormidium papyraceum	r.
Microcoleus chthonoplastes	r.		

This society occurs fairly frequently in the Juncetum Gerardii and in the higher portions of the Spartineto-Distichlidetum, but it can also be found among patches of *Aster subulatus*.

Rivularia-Phaeococcus society. +11·09– ? ft. M.L.W.

Rivularia atra	a.	Gloeocapsa crepidinum	f.–l.a.
R. atra var. confluens	a.	Phormidium corium	o.
Phaeococcus adnatus	a.	P. angustissimum	f.
Microcoleus chthonoplastes	f.	P. tenue	l.o.
Calothrix Contarenii	o.	Lyngbya lutea	o.
Nostoc Linckia	r.	Aphanocapsa marina	r.
Endoderma perforans	f.		

This society, in which the dominant species are *Rivularia atra*, *R. atra* var. *confluens* and *Phaeococcus adnatus*, is common on high marsh bearing a Juncetum Gerardii.

Enteromorpha minima community. – ? +9·4 ft. M.L.W.

Enteromorpha minima	d.	Rhizoclonium tortuosum
E. clathrata f. prostrata		Vaucheria Thuretii
E. intestinalis f. tubulosa		Lyngbya semiplena
Oscillatoria corallinae		L. confervoides
O. subuliformis		Microcoleus chthonoplastes
Phormidium tenue		

This community is abundant, especially in spring and early summer, along the edges of ditches and also on old plants of *Spartina alterniflora* and *S. patens*, whilst it may also be found in patches along the banks of large creeks.

Autumn Cyanophyceae community. +9·09–10·38 ft. M.L.W.

Lyngbya aestuarii	a.	Spirulina labyrinthiformis	l.r.
L. aestuarii var. limicola	a.	Vaucheria sphaerospora	l.r.–f.
L. aestuarii var. spectabilis	a.	V. Thuretii	l.r.
L. aestuarii var. symploceoidea	l.a.	Enteromorpha prolifera f. tubulosa	l.f.
L. confervoides	f.		
L. semiplena	o.	Phaeococcus adnatus	l.f.
Spirulina subsalsa	o.–f.	Phormidium corium	o.–f.

Phormidium autumnale	f.	Rhizoclonium implexum	r.-f.
P. papyraceum	o.	R. tortuosum	f.
P. tenue	o.-f.	Ulothrix implexa	l.o.
Microcoleus chthonoplastes	f.-a.	U. subflaccida	l.r.
Oscillatoria sancta	r.	Urospora isogona	r.

In the late summer, autumn, and early winter this community can be found scattered over the more open portions of the Spartinetum patentis and Spartineto-Distichlidetum, and also on the bare floors of salt pans.

Limicolous Fucaceae. +2·0-9·0 ft. M.L.W.

Fucus vesiculosus ecad volubilis	l.a.[1]	Sphacelaria radicans	f.
F. spiralis var. platycarpus	l.a.	Enteromorpha minima	l.f.
F. spiralis ecad lutarius	l.a.	Ascophyllum Mackaii	l.a.
F. vesiculosus	f.		

Along the edges of creeks *Ascophyllum Mackaii* forms a distinct society, whilst in the Spartinetum alterniflorae *Fucus spiralis* ecad *lutarius* and *F. vesiculosus* ecad *volubilis* are the dominant forms. Where clams or mussels are exposed in the vertical walls of creeks, plants of *F. spiralis* var. *platycarpus* can be found attached to the shells.

Pan association.

Enteromorpha prolifera f. tubulosa
E. compressa f. linearis
E. Hopkirkii
E. intestinalis f. tubulosa
E. minima
E. clathrata f. Linkiana
E. clathrata f. foeniculacea
Percursaria percursa
Chaetomorpha tortuosa
Oscillatoria margaritifera
O. nigroviridis
Calothrix confervicola
Xenococcus Kerneri
Lyngbya confervoides
Lyngbya aestuarii
Rhizoclonium implexum
R. tortuosum
Cladophora gracilis var. vadorum
Ulothrix flacca
Vaucheria dichotoma var. submarina
Monostroma latissimum
Endoderma perforans
Ectocarpus siliculosus
Pylaiella littoralis
Phormidium tenue
P. autumnale
P. papyraceum
Lyngbya semiplena

Evidence in favour of the existence of a pan flora has been adduced elsewhere (Chapman, 1937) and hence need not be reiterated here. Not all the above species will be found in each pool, those cited forming a composite list based on the flora of the pools that were examined.

Comparison with other areas

Similar analyses are available from the salt marshes of Scolt (section V. Chapman, 1939) and also for the marsh at Cold Spring Harbour, Long Island (Johnson & York, 1915). A comparison of those species which are common to both Romney Marsh and the Scolt marshes is set out in Table 9 and the following points can be noted.

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[1] See note published in *Rhodora* concerning the confusion of these two ecological forms in past literature (Chapman, 1938*b*).

Table 9. *Relation of species common to Romney Marsh (Lynn) and marshes of Scolt Head Island, Norfolk, England to the tidal phenomena. Tidal ranges: Lynn 9·2 ft.: Norfolk 16 ft. approx.*

Species	Range Lynn ft.	Range Norf. ft.	Max. submergence per annum Lynn	Max. submergence per annum Norf.	Min. submergence per annum Lynn	Min. submergence per annum Norf.	Max. non-tidal exposure upper level Lynn	Max. non-tidal exposure upper level Norf.	Max. non-tidal exposure lower level Lynn	Max. non-tidal exposure lower level Norf.
Puccinellia maritima	2·29	2·27	372	344	7	82	287	40	8	22
Triglochin maritimum	1·21	2·07	318	372	82	104	24	27	16	20
Algae										
Phacococcus adnatus	1·85	0·6	198	210	0	155	365	30	20	24
Endoderma perforans	1·88	1·4	245	320	7	155	287	30	18	22
Microcoleus chthonoplastes	5·21	2·1	705	340	0	80	365	280	0	22
Phormidium corium	3·49	1·55	599	340	0	125	365	25	1	22
Phormidium autumnale	1·82	2·4	372	385	59	85	26	57	8	8
Lyngbya aestuarii	2·49	1·15	599	220	72	85	24	57	1	23
Vaucheria sphaerospora	1·54	2·3	416	385	101	85	24	40	7	8
Rhizoclonium implexum	2·76	4·0	599	630	115	105	23	37	1	5
Enteromorpha minima	3·33	3·3	705	665	198	325	20	22	0	3
E. prolifera f. tubulosa	7·25	3·25	705	590	198	165	20	22	0	5
Calothrix scopulorum	1·58	1·0	318	305	59	200	26	25	16	22

Max. = upper level. Min. = lower level.

Phaeococcus adnatus. This species occurs wholly on upper marshes in both places where it is subject to long summer exposure, and as the lower limits in both areas are very nearly identical in relation to the tidal phenomena it may be suggested that the lower limits are controlled by the tidal factors.

Endoderma perforans. A species which occurs wholly on upper marshes in both areas, whilst the vertical range is also very similar (1·88 and 1·4 ft.).

Microcoleus chthonoplastes, Phormidium corium, Lyngbya confervoides, L. aestuarii. All have a much wider range on Romney Marsh than they do in Norfolk. There is no agreement in either their upper or lower levels in relation to the tidal factors so that it must be concluded that they are not controlled by the tidal phenomena.

Phormidium autumnale, Vaucheria sphaerospora. The distribution of these two species may be determined by tidal phenomena as the conditions at the upper and lower limits are similar.

		Vertical range ft.	No. of submergences Max. per annum	No. of submergences Min. per annum	Max. period of non-tidal exposure Upper limit days	Max. period of non-tidal exposure Lower limit days
Phormidium autumnale	Romney	1·82	372	59	26	8
	Norfolk	2·4	385	85	57	8
Vaucheria sphaerospora	Romney	1·54	416	101	24	7
	Norfolk	2·3	385	85	40	8

Rhizoclonium implexum, Enteromorpha minima, E. prolifera f. *tubulosa, Calothrix scopulorum.* These species undergo similar tidal conditions at either their upper or lower limits, and so it may be suggested that the tides play some part in controlling their vertical distribution.

		No. of submergences		Max. period of non-tidal exposure	
		Max. per annum	Min. per annum	Upper limit days	Lower limit days
Rhizoclonium implexum	Romney	599	115	23	1
	Norfolk	630	105	37	5
Enteromorpha minima	Romney	705	198	20	0
	Norfolk	665	325	22	3
E. prolifera f. tubulosa	Romney	705	198	20	0
	Norfolk	590	165	22	5
Calothrix scopulorum	Romney	318	59	26	16
	Norfolk	305	200	25	22

Puccinellia maritima, Triglochin maritimum. The lower limits of both species appear to be the same in respect of the number of submergences, whilst the upper limits of *Triglochin* also possess some features in common. For this reason the tides probably play a greater part in determining the range of the latter species rather than that of the former.

		Vertical range ft.	No. of submergences		Max. period of non-tidal exposure	
			Max	Min	Upper limit	Lower limit
Triglochin maritimum	Romney	1·21	318	82	24	16
	Norfolk	2·07	372	104	27	20
Puccinellia maritima	Romney	2·29	372	7	287	8
	Norfolk	2·17	344	82	40	22

The following species common to Romney Marsh and the marsh at Cold Spring Harbour, Long Island, may also be compared, the principal features being shown in Tables 10 and 11.

Vaucheria Thuretii, Chroococcus turgidus, Lyngbya aestuarii, L. lutea, Calothrix scopulorum, Microcoleus tenerrimus, Ulothrix flacca, Enteromorpha minima. All these species occur at much lower levels at Cold Spring Harbour than they do on Romney Marsh, and hence at the former place they undergo greater submergence and less exposure.

Lyngbya semiplena. Although this species occurs at a slightly lower level at Cold Spring Harbour, nevertheless the exposure in both areas is not significantly different.

Microcoleus chthonoplastes, Rhizoclonium tortuosum. In both areas these species go down to levels where they are submerged by every tide, but their upper limits are much lower at Cold Spring Harbour.

Salicornia herbacea, Triglochin maritimum. The vertical distribution of these two species is totally different in the two areas.

Atriplex patula hastata, Distichlis spicata, Limonium trichogonum, Scirpus robustus, Aster subulatus, Juncus Gerardii, Solidago sempervirens. Although these species exist under similar conditions of exposure at their upper limits in both areas, there is no evidence that their vertical ranges are controlled by the tidal phenomena.

Iva frutescens var. *oraria.* The hours exposed per calendar month at both

Table 10. *Relation of the algal species common to Romney Marsh (Lynn) and Cold Spring Harbour (C.S.H.) to the tidal phenomena. Partly after Johnson & York,* 1915. *Tidal ranges: C.S.H.* 7·43 *ft.; Lynn* 9·2 *ft.*

	Levels				Ranges		No. of submergences per annum				Hours submerged per calendar month				Hours exposed per calendar month			
	C.S.H.		Lynn		C.S.H. ft.	Lynn ft.	C.S.H.		Lynn		C.S.H.		Lynn		C.S.H.		Lynn	
	Max.	Min.	Max.	Min			Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Enteromorpha minima	7	—	10·05	6·72	—	3·33	568	—	198	705	97	—	28·7	245·6	639	—	705	488
Vaucheria Thuretii	7	5	10·74	8·44	2	2·3	568	705	82	599	97	275	8·3	145·3	639	461	725	588
Chroococcus turgidus	6·5	—	10·74	9·09	—	1·65	674	—	82	416	161	—	8·3	76	575	—	725	658
Lyngbya aestuarii	7	4	10·8	8·35	3	2·49	568	705	72	599	97	339	6·7	145·3	639	397	727	588
L. semiplena	7·5	6·5	11·05	8·63	1	2·42	400	674	59	564	47	161	5	118	689	575	728	615
Rhizoclonium tortuosum*	8	2	11·06	6·72	6	4·34	242	705	59	705	30	475	5	246	706	261	728	488
Calothrix scopulorum	7	6	11·06	9·48	1	1·58	568	702	59	318	97	203	5	53	639	534	728	680
Lyngbya lutea	7	2	11·09	9·29	5	1·8	568	705	59	372	97	475	5	64	639	261	728	670
Microcoleus chthonoplastes	7·5	4	11·93	6·72	3·5	5·21	400	705	0	705	42	339	0	246	689	397	734	488
M. tenerrimus	6·5	—	11·93	9·47	—	2·46	674	—	0	318	161	—	0	53	575	-	734	680
Ulothrix flacca	6·5	3	12·41	8·44	3·5	3·97	674	705	0	599	161	398	0	145	575	339	734	588

Ft. above M.L.W. Max. = upper level. Min. = lower level.

* As *Chaetomorpha tortuosa* at C.S.H.

Table 11. *Relation of the phanerogam species common to Romney Marsh (Lynn) and Cold Spring Harbour (C.S.H.) to the tidal phenomena. Partly after Johnson & York,* 1915. *Tidal ranges: C.S.H.* 7·43 *ft.; Lynn* 9·2 *ft.*

	Levels				Ranges		No. of submergences per growing season				Hours submerged per calendar month				Hours exposed per calendar month			
	C.S.H.		Lynn		C.S.H.	Lynn	C.S.H.		Lynn		C.S.H.		Lynn		C.S.H.		Lynn	
	Max.	Min.	Max.	Min.			Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Aster subulatus	9	7·25	12·6	10 6	1·75	2·0	10	229	0	55	2·08	72	0	11·4	734·4	664·3	733·7	722·3
Atriplex patula var. hastata	8·5	6·0	12·0	?10·6	2·5	?1·4	30	351	0	?55	8·7	203	0	?11·4	727·8	533·6	733·7	?722·3
Distichlis spicata	8·25	6·5	11·3	9·0	1·75	2·3	65	337	18	233	16·8	161	1·95	90·4	719·7	575·5	731·0	643·3
Iva frutescens var. oraria	8·5	7·5	12·5	11·0	1	1·5	30	200	0	33	8·7	47·2	0	5·0	727·8	689·3	733·7	728
Juncus Gerardii	12 +	9	11·7	9·75	3 –	1·95	0	10	5	131	0	2·08	0·3	45·7	735·5	734·4	733·4	688
Limonium trichogonum*	8·25	7·25	11·9	8·35	1·0	3·55	65	229	0	308	16·8	72	0	145·3	719·7	664·3	733·7	588·4
Plantago oliganthos†	8·25	6·25	10·1	8·6	2·0	1·5	65	343	37	292	16·8	177	22	118·2	719·7	559·5	711·7	615·5
Salicornia herbacea	7·5	6·5	10·7	9·7	1·0	1·0	200	337	43	131	47·2	161	8·3	45·7	689·3	575·5	725·4	688
Scirpus robustus	8·5	7·0	12	10·1	1·5	1·9	30	284	0	87	8·7	97	0	22	727·8	639·5	733·7	711·7
Solidago sempervirens	12 +	6·5	12·4 –	10·8	5·5	1·6	0	337	0	43	0	161	0	8·3	735·5	575·5	733·7	725·4
Spartina alterniflora	6·5	1·5	10·7	2 8	5·0	7·9	337	355	43	355	161	497	8·3	495·9	575·5	239·2	725·4	237·8
Spartina patens var. juncea	8·25	6·5	12·3	7·8	1·75	4·5	65	337	0	350	16·8	161	0	192·7	719·7	575·5	733·7	541·0
Suaeda maritima	8	6·5	11·3	8·6	1·5	2 7	121	337	18	292	30 4	161	1·95	118·2	706·1	575·5	731	615·5
Triglochin maritimum	7·5	6·25	10·7	9·5	1·25	1·2	200	343	43	168	47·2	177	8·3	53·4	689·3	559·5	725·4	680·3

Ft. above M.L.W. Max. = upper level. Min. = lower level.

* As *L. Carolinianum* at C.S.H. †As *P. decipiens* at C.S.H.

the upper and lower limits in the two areas are similar (727·8, 733·7 hr.: 689·3, 728 hr.). and it is possible that the latter may therefore be controlled by the degree of submergence.

Plantago oliganthos. This is the only species which grows under closely similar tidal conditions in the two areas.

	No. of submergences per growing season		Hours submerged per calendar month		Hours exposed per calendar month	
	Upper limit	Lower limit	Upper	Lower	Upper	Lower
C.S.H.	65	343	16·83	177	719·7	559
Romney	87	292	22	118	711·7	615

Spartina alterniflora, *S. patens* var. *juncea*, *Suaeda maritima*. These species undergo the same tidal conditions at their lower limits in both areas, and this suggests that the tidal phenomena control the lower limit of their vertical range.

	No. of submergences per growing season Lower limit		Hours submerged per calendar month Lower limit		Hours exposed per calendar month Lower limit	
	C.S.H.	Romney	C.S.H.	Romney	C.S.H.	Romney
Spartina alterniflora	355	355	497	496	239	238
S. patens	337	350	161	193	575	541
Suaeda maritima	337	292	161	118	575	615

It seems characteristic of the American species that *the farther south they spread on that continent the more tolerant they are of submergence* (i.e. the lower they go in relation to the tidal plane). This may be a temperature relationship, and it suggests strongly that tidal phenomena, *per se*, are not entirely responsible for the determination of vertical ranges.

In conclusion it may be pointed out that it is only by means of comparisons such as these, however inadequate they may be, that one can obtain information about the operation of certain factors, in this case the tidal phenomena, upon the distribution of the various species. It is not pretended that the suggestions made in these last few paragraphs are other than tentative and it is hoped that other workers will take up the problems that now present themselves.

The material contained in these two sections was obtained whilst the author held a Henry Fellowship at Harvard. His thanks are due to Prof. Redfield and the Staff of the Biological Laboratory at Harvard for the facilities provided and to Prof. Fernald for valuable assistance in the systematics.

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PHYSIOLOGICAL AND ECOLOGICAL STUDIES ON AN ARCTIC VEGETATION

I. THE VEGETATION OF JAN MAYEN ISLAND

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(*With Plates* 10 *and* 11 *and two Figures in the Text*)

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GENERAL INTRODUCTION

WITH but few exceptions the botanical investigations undertaken by scientific expeditions in western arctic regions have been confined to systematic collecting and descriptive ecology. Thus, while much valuable information is available about the distribution of species and the composition of the vegetation in such regions as Spitzbergen and Greenland,[1] comparatively little is known with regard to the effect of the environment on the metabolic processes which determine growth. In view of this situation it was decided that the botanical work of the Imperial College Expedition to Jan Mayen in 1938[2] should include a physiological study of the factors controlling growth in the arctic. These investigations were complementary to the collection of plant specimens and an ecological description of the vegetation, since it is only by considering these aspects together that general conclusions can be drawn.

The present paper contains a description of the vegetation of the island together with geographical and climatic data. In subsequent communications the physiological results will be presented, though the general scope of the work will be indicated here.

During the course of a short summer expedition it would clearly be possible to collect only preliminary information on some of the more important problems and it was decided therefore to direct attention primarily to two points of physiological importance, (i) the levels of soil nutrients and their relationship to the growth of the vegetation, and (ii) the effect of the short growing season, during which light is continuous, on carbohydrate metabolism. These problems were selected for the following reasons.

Much detailed research in temperate regions has shown that an adequate supply of mineral nutrients, especially nitrogen, phosphorus and potassium is essential for plant growth. Nitrogen is particularly important and the effects of its deficiency completely mask the effects of a lack of other nutrients (Gregory, 1937). Nitrogen in the soil is derived mainly from the decomposition of pre-existing vegetation and from the activity of certain micro-organisms. In the arctic vegetation is sparse, and moreover the low soil temperature during the greater part of the year curtails the activity of soil organisms. For these reasons it appeared probable that in the arctic, the nitrogen level would be low and that it might be a controlling factor in plant growth. Furthermore, in areas frequented by seabirds, where the nitrogen level would be higher, the vegetation was reported to be more luxuriant (Summerhayes & Elton, 1928; Polunin, 1934).

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[1] Owing to the inaccessibility of numerous Russian publications and the language difficulty the writers have been unable to determine definitely the extent of physiological investigation in Russian arctic territory, but almost no work of this type is, however, reported in the *Transactions of the Arctic Institute of U.S.S.R.* or in recent numbers of *Comptes Rendus of the Academy of Science of the U.S.S.R.*

[2] A general description of the work of the Expedition is given by King (1939).

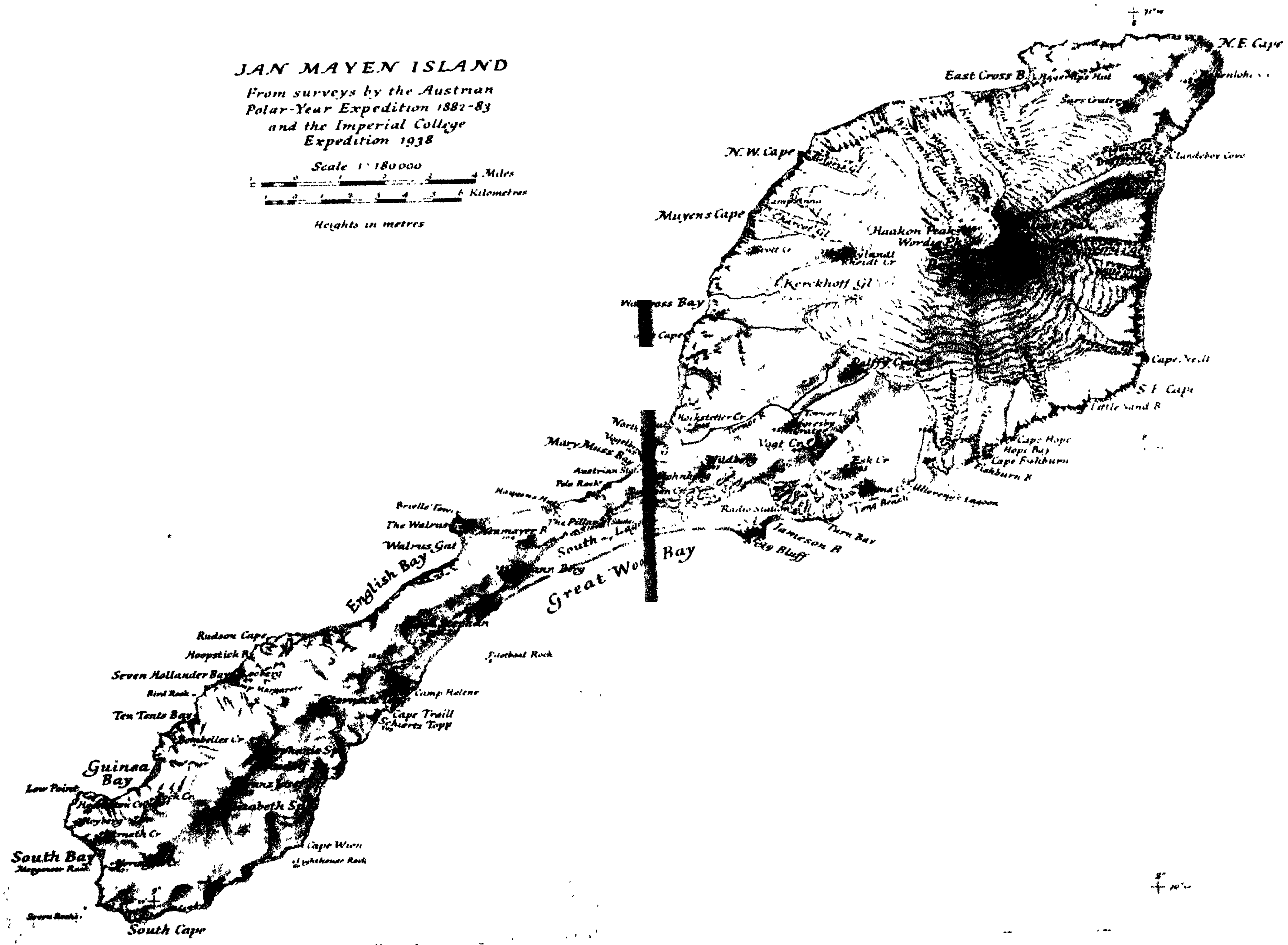

Fig. 1. Map of Jan Mayen Island. Reproduced on a redu[redacted] scale by permission of the Royal Geographical Society.

As it was known before leaving England that there were large bird colonies on Jan Mayen, the necessary equipment for the study of soil nitrogen in relation to plant growth was taken on the expedition. The greater luxuriance of the vegetation in situations enriched by the droppings of animals indicated the expected correlation between nitrogen supply and plant growth and a detailed study was accordingly made to establish the importance of this factor. Soil samples were collected from localities supporting a wide range of vegetational types. Chemical analyses were carried out (the soluble nitrogen values were determined at the time of sampling) and the micro-fauna and flora were also studied. The results are given in the second of this series of papers. It should be mentioned that little of this information could have been obtained without the co-operation of workers in this country who have, with their special knowledge, examined the samples brought home by the expedition.

The arctic environment is characterized by a short growing season during which temperatures are comparatively low and light is continuous. Conflicting views have been advanced as to the effect of these conditions on carbohydrate metabolism, and to shed further light on this important question it was decided to attempt some measurement of assimilation, and also to determine the changes in the carbohydrate content of plants during the growing season. It was clearly of paramount importance to determine the manner in which plants respond to the prevailing conditions of continuous daylight; accordingly the diurnal movement of stomata as well as changes in carbohydrate throughout the day were studied. These investigations will be reported in a later paper.

The limitations of the present investigations should be emphasized. The entire field work occupied less than 7 weeks, and some of that time had to be devoted to the establishment of camps and the transport of equipment as well as to general exploration. The results are therefore to be regarded merely as a preliminary survey; they show however that the accurate physiological methods necessary for the elucidation of these problems can be employed with success despite the restrictions necessarily imposed by expedition conditions.

GEOGRAPHY

Jan Mayen is situated in the Greenland Sea at latitude 70° 50′-71° 10′ N. and 8-9° W. of Greenwich. Greenland, the nearest land, is some 200 miles to the west, while Iceland is about 250 miles south. The island is small (Fig. 1), less than 35 miles long and varying in width from 2 to 10 miles; thus for its area the length of the coastline is considerable. Steep cliffs, frequented in summer by large numbers of sea birds, form the greater part of the coast. Almost all the interior of the island is mountainous and, at the northern end the Beerenberg, an extinct volcano now heavily glaciated, rises to the height of 2340 m.[1] The central part of the island is less rugged but in the south peaks up to 900 m. occur; these are however not glaciated and during the summer snow lies only in occasional patches. The greater part of the snow below 800 m. has melted by mid-June but even close to the coast some patches remain till August. In September or October the winter snowfalls commence.

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[1] Height as determined by the 1938 Expedition.

So far as is known the island is entirely volcanic in origin (Wordie, 1926). At the present day the only signs of activity are occasional earthquakes and some small steam vents on Egg Bluff. Volcanic activity on a considerable scale has however been observed as recently as 1818 when Scoresby saw dust eruptions from small craters on the south-west flank of Beerenberg. The main crater has however been extinct for a considerable period.

From the biological viewpoint perhaps the most interesting aspect of the island's geology is that no signs of ice erosion are found apart from the glaciation now in progress on Beerenberg. All the land forms of the central and southern part of the island are typical of volcanic country, consisting of cones and lava flows. Thus it appears that the island in its present form originated since the retreat of the Quaternary ice sheet. There is no definite evidence as to when the island was last completely sterilized by volcanic activity but the above facts indicate that plant colonization occurred at a comparatively recent geological date.

The most common rocks are trachybasalts (Wordie, 1926), which yield little soil by weathering, and the porous nature of the lavas allows very rapid drainage. These conditions, as will be shown later, militate against the development of vascular plants. A considerable thickness of basaltic tuffs are found underlying the lavas near the base of the southern flank of Beerenberg. In such localities a much finer and more retentive soil is formed. Trachite and andesite, probably of greater age than the other rock types, also occur.

The small size of Jan Mayen and its remoteness from larger land masses appear to have discouraged scientific parties from visiting the island. The first scientific expedition of note was the Austrian Polar Year Expedition of 1882–3, which prepared a map of the island. Despite the inaccuracy of this chart, especially in the northern and southern extremities of the island (where it was based on observations from the sea), it remained the standard map of the island until 1938. Other expeditions have been referred to by Wordie (1922) and King (1939). It need only be stated here that while most of the island had been travelled over with the exception of the northern side of Beerenberg, little detailed scientific work had been published and botanical publications consisted solely of descriptions of plants collected. The fullest lists are those of Bird (1935) for vascular plants and Gandrup (1924) for bryophyta and lichens. A detailed study of lichens from the island has recently been made by Lynge (1939) who has recorded no less than 144 species. The present communication appears however to be the first attempt at a general ecological description of the island.

CLIMATE

Since this series of papers is concerned with the effects of the environment on plant growth it is essential to describe the climate of the island in some detail. With the exception of the light intensity figures all the data presented here are from the observations of the Jan Mayen Meteorological and Wireless Station which was established in 1921 and is under the control of Vaervarslingen for Nord Norge, Tromsø. This Station together with those at Myggbukta (Greenland), Spitzbergen and Bear Island fill an important space in the world's weather map, their reports being of great value in weather forecasting in the North Atlantic. Some of the records not yet published have been generously provided by the Director of the service in Tromsø.

Temperature. No soil temperatures are available except a few sporadic observations, so that air temperatures will alone be considered. The average air temperatures for June, July, August and September during the period 1924–33 were 3·0, 5·8, 6·1 and 3·6° C. respectively with an annual mean of 0·1° C. The coldest month was March with a mean temperature of −4·2° C. This comparatively small annual variation in temperature is in accordance with the oceanic climate. Diurnal variations during the summer are also small. In July and August, 1938, the maximum daily fluctuation was 5·5° C. and the minimum 1·0° C. The maximum and minimum temperatures for the period were 11·5 and 1·0° C. respectively with a mean of 5·9° C.

Evidence that the climate of Jan Mayen is becoming warmer is provided by a comparison of the observations of the Austrian Expedition of 1882–3 with those of recent years. The mean summer temperature in 1882–3 was 2·6° C. with an annual mean of −2·3° C. These are 2·0–3·0° C. lower than the present-day values. It will be interesting to see what effect the increasing temperature has in the future on the vegetation of the island.

Wind. Probably the most important climatic factor influencing the distribution of vegetation on the island is wind. It will be seen from Table 1 that winds of considerable force are very prevalent.

In Table 1 are shown the percentages of the total time when winds of various strengths were blowing. Even in the summer months wind of greater

Table 1. *Force of wind on Jan Mayen Island*

Data from Iversen (1936)

Beauford no.	Miles per hour	June	July	August	Yearly average
0	0–1	6·7	6·4	7·2	5·0
1–3	2–11	54·0	54·5	56·4	42·0
4–5	11–21	27·8	28·0	24·2	29·4
6–7	22–33	9·6	8·5	9·2	15·7
8–9	34–48	1·7	2·6	2·4	5·8
10–12	Over 48	0·2	0·0	0·6	2·1
		100·0	100·0	100·0	100·0

The percentage of the total time during which wind of each force was recorded is given for the years 1924–33. Four observations were made daily.

speed than 22 m.p.h. prevailed for over 11 % of the time. Winds of force 12 (over 65 m.p.h.) are not exceptional especially in winter. During the summer the prevailing directions are easterly and north-westerly, while southerly winds are uncommon. It should be mentioned that the Meteorological Station, where the observations were made, is in an exposed situation so that in the sheltered vegetated areas the wind speed would have been much lower.

Fog and cloud. Especially in summer, conditions of fog and mist are common on Jan Mayen and the sky is almost perpetually overcast. This is clearly seen in Table 2. At the Meteorological Station in Jameson Bay, fog is probably somewhat less prevalent than in the south-west part of the island. The high relative humidity shown below and the rather low light intensities (Table 3) are due to these conditions.

Table 2. *Occurrence of fog and cloud and the amount of precipitation on Jan Mayen Island*

	No. of days			
	Fog and mist	Bright	Overcast	Precipitation in mm.
June	15	1·25	19	25·0
July	15	0	25	63·5
August	12	0	23	45·5
September	9	0	18	68·7
Annual mean	90	4	232	587·3

Averages for 1933–6 (from *Jahrbuch des Norwegischen Meteorologischen Instituts*, Oslo.)

Precipitation. The precipitation during the summer months and the annual mean for 4 years are given in Table 2. Large variations occur from year to year especially in the summer months. Much of the precipitation in June–September is in the form of mist and light rain, heavy rain being rare; in July and August 1938, 10 mm. or more fell on only 5 days.

Humidity of the atmosphere. The relative humidity is usually high. An analysis of the readings taken three times daily in July and August 1938 shows the following:

Relative humidity	for % of the total observations
100	42·3
90	24·7
80	24·2
70	7·2
60	1·5
Less than 60	Nil

Light intensity. The only light-intensity values which are available were taken during the 1938 Expedition in connexion with work on stomatal aperture. As the observations were made at varying times they have been grouped in 2 hr. periods (Table 3). It will be seen that very considerable fluctuations occurred as a result of clouds. The determinations were made with a Weston

Photronic cell (Model No. 594) which was placed on the ground beside the plants in such a position that the light falling on the cell was similar to that falling on the leaf under examination. Had the cell been held in a horizontal position above the ground consistently higher values would have been obtained. Furthermore, the observations were all made on a slope facing south in Fishburn Valley. The Beerenberg, rising behind, will have reduced considerably the values taken between 7·00 p.m. and 5.00 a.m. These facts should be borne in mind when comparing the values with those for other regions.

Table 3. *Light intensities in foot-candles. Jan Mayen Island*, 1938

		Midday			Midnight		
		11.00 a.m.– 1.00 p.m.	3.00– 5.00 p.m.	7.00– 9.00 p.m.	11.00 p.m.– 1.00 a.m.	3.00– 5.00 a.m.	7.00– 9.00 a.m.
9–16 July	Max.	3200	2500	875	288	550	1450
	Min.	900	635	400	25	225	575
	Mean	1700	2500	556	141	404	890
20–28 July	Max.	1600	2400	425	125	275	700
	Min.	850	260	225	5	100	230
	Mean	965	992	344	32	188	401
15–20 August	Max.	2400	1700	484	2·5	175	1012
	Min.	1250	670	50	1·5	75	377
	Mean	1580	1230	353	2·2	75	796

FLORA

The vascular flora of Jan Mayen is small and contains, so far as is known, only 58 species of vascular plants, trees and shrubs being absent except prostrate forms of *Salix herbacea* and *Empetrum nigrum*. The collection made by the Imperial College Expedition may be regarded as fairly representative and contains 15 species not previously recorded for the island. The collections of lichens and bryophyta were, however, rather scanty and this section of the Jan Mayen flora especially would repay further study. The collections have been placed in the herbarium of the British Museum, and a list has been published in the *Journal of Botany* (Russell *et al.* 1940). The vascular plants were identified by Mr A. J. Wilmott, the mosses by Mr W. R. Sherrin and the lichens by Mr I. Mackenzie Lamb to whom the present authors are much indebted.

For fuller information with regard to the lichens and bryophyta on Jan Mayen reference should be made to Gandrup (1924) and Lynge (1939).

TYPES OF VEGETATION

(1) *General characteristics*

Before attempting to classify the vegetation of Jan Mayen a few general observations about the region as a whole should be made. Broadly speaking the environmental conditions were unfavourable for the growth of vascular plants. A thin covering of soil, through which drainage was extremely rapid, coupled with exposure to frequent strong winds (Table 1) militated against the development of vascular plants and over wide areas the vegetation was composed principally of mosses with occasional stunted phanerogams.

In limited areas, however, more favourable conditions prevailed. Shelter from winds and a more abundant water supply associated in some cases with a greater depth of soil permitted the development of a more luxuriant vegetation. These conditions were realized especially in the Fishburn district, a region facing south and sheltered to a large degree by the slopes of Beerenberg rising behind it. The surface layers, consisting of well weathered tuffs, provided an abundant soil and in consequence drainage was less rapid than elsewhere. Moreover, springs and streams fed by the snowfields and glaciers on the upper slopes maintained an adequate water supply.

The effect of bird droppings and to a less extent those of arctic foxes was very marked. Crevices on moist bird cliffs and the slopes below them bore well-developed vegetation in contrast to regions physiographically similar but where this factor was not operative.

Vegetation occurred over an altitudinal range from sea level to 700 m. while in one locality vascular plants were found at an altitude of 1500 m. By comparison with temperate regions there was little zonation of the vegetation with altitude. This is due to the absence of lowland communities of the types found in lower latitudes. No species of vascular plants were restricted to high situations and only two, *Halianthus peploides* and *Mertensia maritima*, both maritime plants, occurred only on the coast. Other plants had a varying altitudinal amplitude. Comparatively few were confined to any one particular type of locality, and the same plants played a leading part in many different situations. As insufficient work was carried out on bryophytes and lichens it cannot be stated whether they showed a greater zonation but this is not improbable.

(ii) *Classification and description of the types of vegetation*

To attempt an elaborate classification of the vegetation into plant communities would be impracticable and moreover would not serve the purpose of the present investigation which was to study the general features of the arctic environment rather than to furnish a description in great detail of a limited area.

The vegetation has been divided into broad types in the determination of which the nature both of the habitat and of the vegetation have been taken into account. Each type should be regarded not so much as a single unit but as a group of closely allied units. The types are comparable to the *ecosystems* which Seidenfaden & Sørensen (1937) have defined for north-east Greenland.

Three categories of types have been distinguished, namely, general, localized and those controlled by biotic factors.

A. *General types covering wide areas.*

General types were those covering large areas and consequently responsible for the characteristic landscape. For their development no specially modified conditions were required. Seven such types are here described:

(1) Lava fields.
(2) Exposed hillside: dry-moss communities.
(3) Exposed hillside: wet-moss communities.
(4) Moist slopes on weathered basaltic tuffs.
(5) Open rocky ground.
(6) Volcanic desert.
(7) Sandy beach.

(1) *Lava fields.* A large part of the surface of the island consisted of lava flows (Pl. 10, phot. 1) showing varying degrees of erosion. Such areas, where the original "ropy" nature of the lava was still preserved, are considered under this heading. On account both of the nature of the lava and the local conditions the surface layers were characterized by extreme porosity and a paucity of soil. Colonization by vascular plants was extremely slow and it was possible to distinguish a number of successional stages.

(*a*) An early stage was found at North-West Cape, Seven Hollanders Bay and several other localities in the southern part of the island. Vascular plants were almost entirely absent and the fields consisted of loose blocks and hollows covered with a dense growth of foliaceous lichens with occasional mosses. The following were among the most common lichens:

Peltigera malacea var. polyphylla
Cladonia mitis
C. rangiferina
C. uncialis
C. coccifera
Cladonia elongata f. ecmocyna
Stereocaulon denudatum var. umbonatum
Ochrolechia frigida
Cornicularia aculeata
Sphaerophorus globosus

(*b*) A later stage in the development of the vegetation was found at West Cross Bay and Guinea Bay. It is regretted that sufficient geological evidence is not available to assess the relative ages of the various lava fields. Foliaceous lichens were here less in evidence and mosses were dominant, including *Rhacomitrium lanuginosum*, *Webera cruda* and *Dicranum congestum*. A number of vascular plants grew in the moss carpet, notably:

Salix herbacea
Luzula confusa
Cerastium alpinum
C. cerastioides
Saxifraga caespitosa
S. oppositifolia
Festuca rubra

In some situations *Salix herbacea* formed close mats almost to the exclusion of the mosses.

Apart from this general type of vegetation a more advanced type occurred in consolidated hollows which will be described later.

(2) *Exposed hillsides: dry-moss communities.* This was the most extensive type of vegetation on the island and was typical of the well-drained hillsides which form the greater part of the island, excluding only the Beerenberg massif. Such slopes were characterized by a high degree of exposure, a poorly developed soil and rapid drainage.

The dominant species were the mosses *Rhacomitrium lanuginosum*, *R. canescens*, and less frequently *R. fasciculare*. On the partially sheltered slopes mosses formed a uniform carpet broken only by occasional large stones, while on the edges of ridges and other particularly exposed situations the moss covering was usually not complete and there were patches of bare ground. It was frequently observed on unbroken areas of moss that there were narrow bands of dead tissue. Such bands formed a variable pattern of circles and curves. It is difficult to offer an explanation of these as their form excluded the possibility that they were due to fungal attack. As a speculation it may be suggested that they resulted from the disruption of the tissue by a freeze-thaw process during the winter, the mechanism perhaps resembling that by which soil polygons develop.

The vascular plants growing among the mosses were usually stunted, and the most common species were:

Ranunculus glacialis
Cerastium alpinum
Saxifraga caespitosa
S. oppositifolia
S. tenuis
Saxifraga nivalis
Polygonum viviparum
Oxyria digyna
Salix herbacea

Salix herbacea was frequently present in considerable abundance forming straggling mats in the moss. On the more broken and unstable ground *Saxifraga oppositifolia* and *Ranunculus glacialis* were often dominant.

A number of other species occurred, usually less commonly, but it was impossible to assess their relative frequencies as they varied considerably from place to place:

Draba alpina
D. arctica
Silene acaulis
Sagina nivalis
S. cf. caespitosa
Saxifraga cernua
Luzula confusa
Carex lagopina
Poa pratensis
P. alpina
Festuca rubra
F. vivipara

Less frequently met with and confined to limited areas were:

Cardamine bellidifolia
Draba nivalis
Alsine biflora
A. rubella
Cassiope hypnoides (one exceptional locality)
Calamagrostis neglecta
Trisetum spicatum

In addition a number of plants more truly belonging to neighbouring types were found from time to time. Numerous small areas showed vegetation intermediate between this and the various localized types to be considered later.

(3) *Exposed hillsides: wet-moss communities.* This type of vegetation covered a wide area from Cape Traill to South West Cape on the southern side

of the island. The vegetation was dominated by mosses of a more hygrophylous type than those found in other localities and included species of *Hypnum*. It is on this account separated from "dry-moss communities" already described. The distinction between this and the former type appears to be due to climatic rather than physiographic or edaphic factors. As in the former type the substratum consisted of porous material and there was little soil. Heavy mists, a general characteristic of the climate of the island were particularly frequent in this region, and the precipitation was possibly higher. This locality could unfortunately not be studied in as great detail as the other areas. During the time it was visited perpetual mist restricted visibility usually to a few metres, and it would be unwise with the present data to discuss its relationships in greater detail. The only collection of *Cardamine pratensis* was from a community of this type, but in general vascular plants played a very small part in the vegetation; *Saxifraga foliolosa* was perhaps the most common species.

(4) *Moist slopes on weathered basaltic tuffs.* This type was developed best in the Fishburn district in which the edaphic conditions were unusually favourable for the reasons already given. Vascular plants were dominant, and while the vegetation contained many species found also in the "dry-moss communities", they were here represented by larger and better-developed individuals. This community occupied the eastern flank of the Fishburn Valley but elsewhere it was rare and restricted to small areas usually at the foot of slopes.

The characteristic vascular plants were:

Salix herbacea	d.-cd.	Saxifraga nivalis	f.
Equisetum arvense	d.-cd.	S. cernua	f.
Polygonum viviparum	a.	Draba alpina	f.
Oxyria digyna	a.	D. arctica	o.
Ranunculus glacialis	a.-f.	Carex Bigelovii	f.-o. (moister places)
R. pygmaeus	a.-f. (moister places)	Festuca rubra	o.
Cerastium alpinum	a.	Poa pratensis	o.
C. cerastioides	a.-f.	Trisetum spicatum	o.-r.
Saxifraga caespitosa	f.	Potentilla alpestris	r.-absent
S. tenuis	f.		

Salix herbacea, which occurred in almost every type of vegetation was usually dominant in the drier situations while, with poorer drainage, *Equisetum arvense* became dominant or codominant.

Mosses, including *Dicranoweisia crispula*, *Rhacomitrium lanuginosum*, *R. canescens*, *Tetraplodon mnioides*, *Aulacomnium turgidum*, *Bryum* sp. and *Hypnum* sp. were important especially in moist places. The lichens *Stereocaulon alpinum*, *S. denudatum* and *Peltigera canina* were also present.

(5) *Open rocky ground* (including stabilized moraines). Considerable areas of well-drained open stony ground occurred, especially on the slopes of Beerenberg. The vegetation was open and in the steeper places, where the ground was little consolidated the main species were:

Ranunculus glacialis
Silene acaulis (especially near the coast)
Luzula confusa
Polygonum viviparum
Cerastium alpinum
Saxifraga caespitosa
S. oppositifolia

Under the shelter of stones in moist pockets mosses such as ***Webera cruda*** were found together with *Oxyria digyna.*

On flatter and more stabilized areas occasional large mats of ***Empetrum hermaphroditum*** (Pl. 10, phot. 2) and *Salix herbacea* occurred. In some cases the stems of *Empetrum* reached a diameter of 8 or 9 cm. and were the most woody plants on the island.

An abundant development of crustaceous lichens included the following species:

Lecidea pantherina
L. pelobotryon
Toninia leucophaeopsis var.
Lecanora polytropa
Placopsis gelida
Alectroria nigricans
Caloplaca elegans

Several species of *Stereocaulon* and *Cetraria* also occurred.

(6) *Volcanic desert.* The debris from dust eruptions of comparatively recent date, and conveniently styled "volcanic deserts", consisted of small cinder cones 2–5 m. high which rose from level stretches of fine sandy ash (Pl. 11, phot. 3). Two such regions were examined. At Jameson Bay an area of this type was believed to be the result of an eruption early in the nineteenth century—the most recent volcanic activity on the island. North-west of Cape Traill was a similar region but probably of greater age.

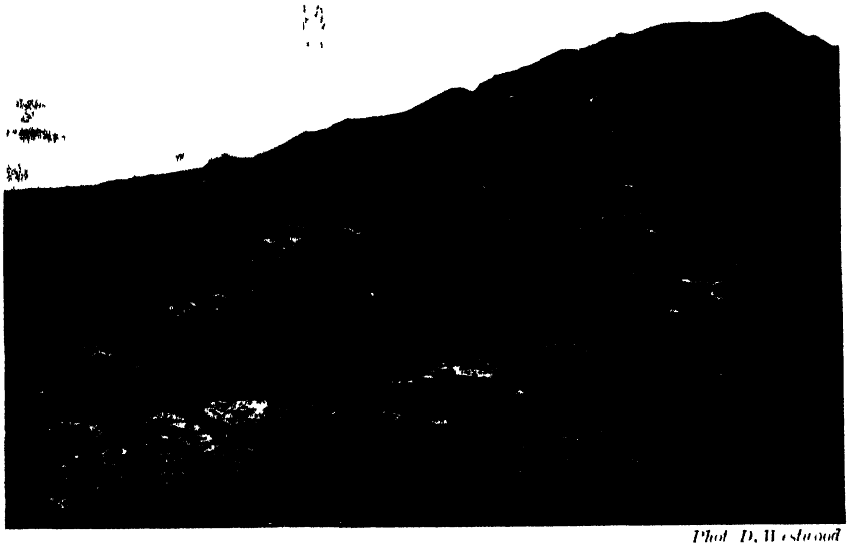
The Jameson Bay area was incompletely consolidated, and the flat areas between the cones were undermined in many places by large cavities so that the surface crust collapsed when walked upon. Surface drainage was for the most part rapid though the water table was less than 2 m. below the surface. A very sparse vegetation, confined to the cones, consisted of occasional plants of the following species:

Oxyria digyna
Cochlearia groenlandica
Cerastium alpinum
Ranunculus glacialis
Sagina caespitosa
Saxifraga caespitosa
Draba alpina
D. arctica
Poa alpina var. vivipara

Bryophyta and foliaceous lichens were absent and crustose lichens were rare.

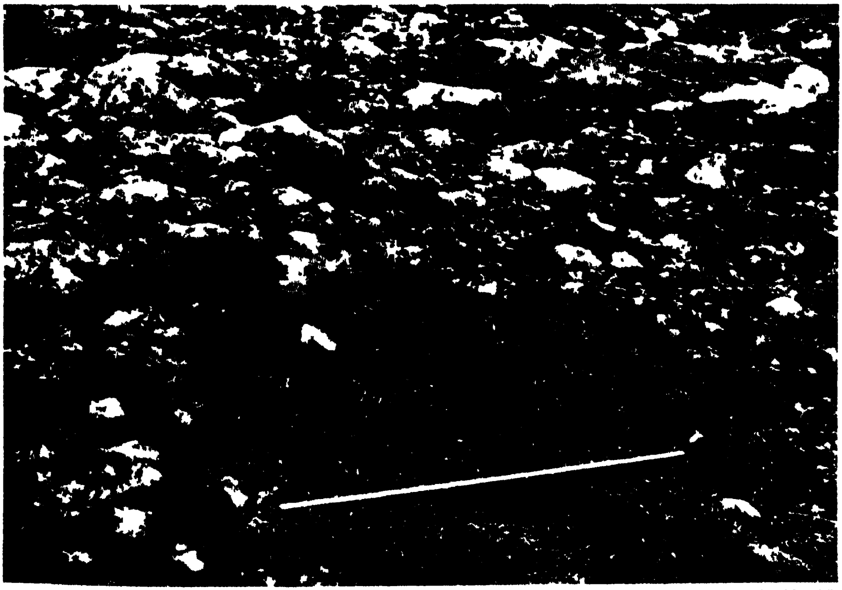
Vegetation on the "desert" near Cape Traill was at a more advanced stage of development. In addition to the above-mentioned species *Salix herbacea*, *Saxifraga caespitosa*, *S. oppositifolia* and *Luzula confusa* were collected. In the more stable areas small patches of closed vegetation were dominated by *Salix herbacea* and mosses (mainly *Rhacomitrium* spp.). By contrast with the other types of vegetation on volcanic material, lichens and bryophyta played no part in the primary colonization.

(7) *Sandy beaches.* The vegetation proper of sandy beaches consisted largely of *Halianthus peploides* and *Mertensia maritima* but occasionally the sand-binding *Carex incurva* was present. In the neighbourhood of bird cliffs these species were especially well developed and numerous but elsewhere they



Phot. D. Westwood

Phot. 1. Typical lava-field, Jan Mayen Island, vegetation mainly crustaceous lichens.



Phot. R.S.R. No. 35

Phot. 2. *Empetrum hermaphroditum* on open rocky ground of Jan Mayen Island, with 1 m. scale in foreground.

were smaller and infrequent. Where outwash streams made conditions more moist *Oxyria digyna* and *Cochlearia groenlandica* occurred.

Perhaps the most striking feature of the beaches on Jan Mayen was the large amount of driftwood found on all parts of the coast. Samples brought back have been examined by Dr F. Y. Henderson who identified them as follows:

Salix sp.	4 samples	Five-leaved pine	2
Spruce	24	Tsuga canadensis	1
Larch	14		

The large amount of spruce and larch together with the absence of *Pinus sylvestris* suggests that the major drift is from Northern Europe or Asia. It is surprising that no birch was found as it grows commonly with spruce and larch. The single specimen of *Tsuga canadensis* was the sole indication of drift from the south-west.

B. *Localized types*

In limited areas within the general types described above the vegetation was modified on account of special conditions of water supply, drainage, shelter, snow effect or other causes. The resulting vegetation has been classified into eleven localized types which are described below. For reasons of convenience the types in the development of which biotic factors were important will be considered separately. The main "localized types", and the conditions under which they developed, are:

- (*a*) Wet situations.
  - Type 8. Edges of streams and pools.
- (*b*) Moist sheltered situations.
  - Type 9. "Sibbaldia" banks.
  - 10. Consolidated hollows in lava fields.
- (*c*) Polygons and solifluxion areas.
  - Type 11. Active stone polygons.
  - 12. Stabilized stone polygons.
  - 13. Solifluxion areas.
- (*d*) Unstable ground.
  - Type 14. Moist earth slides.
  - 15. Screes and moraine slopes.
- (*e*) Snow effect.
  - Type 16. Late snow areas.
- (*f*) Other conditions.
  - Type 17. Alluvial gravel beds.
  - 18. Steam vent.

(8) *Edges of streams and pools.* Owing to the porous nature of the ground, streams and pools were of infrequent occurrence. In consequence the special

vegetation which developed contiguous to water was rarely met with and none of the areas studied was extensive.

None the less a most distinctive type of vegetation was developed and one species of vascular plant, *Ranunculus hyperboreus* was confined to such situations.

With the solitary exception referred to below, mosses were always dominant, forming a lush carpet, *Hypnum uncinatum* being the most common species. At the edges of streams where water was moving slowly through the moss, and the surface of the moss was but a few cm. above the water table, *Koenigia islandica* was usually the only vascular plant in the moss bed. This noteworthy little plant was the sole annual found on Jan Mayen.

In slightly drier moss *Catabrosa algida* occurred, and a little further from the moving water *Ranunculus hyperboreus* was often met with in great abundance. A number of other plants occurred commonly in somewhat less swampy situations and are given below in the approximate order in which they appeared from the dampest localities outwards:

Saxifraga rivularis
Cochlearia officinalis
Saxifraga foliolosa
Calamagrostis neglecta
Carex Bigelovii
Ranunculus pygmaeus

Occasionally, as in a hollow on the north side of Wildberg, wet localities were met with from which moss was absent. Here, scrambling over mud, *Ranunculus hyperboreus* occurred alone with a more straggling habit and longer petioles than when growing among moss (Herbarium Sheet No. 214 in the Expedition collection). In a somewhat similar region near Fishburn the liverwort *Marchantia polymorpha* was recorded.

(9) "*Sibbaldia*" *banks*. The most luxuriant growth and the greatest number of phanerogams, apart from the biotic types to be discussed later, occurred on sheltered and fairly moist banks. On account of the fact that *Sibbaldia procumbens* was in the main confined to these banks and often dominant there, "*Sibbaldia*" bank has been used as a convenient name for this type of vegetation. In size the banks varied from small slopes a few square metres in extent to those 5 or 6 m. high and of considerable length. Banks of this type were found in several parts of the island and were best developed at Fishburn. Shelter from wind, an adequate moisture supply, good drainage and an accumulation of soil all played a part in determining the vegetation and the most luxuriant growth occurred on banks facing south. The importance of the winter-snow covering in the development of this type of vegetation will be considered later in this paper. A number of species were confined to this type of vegetation and those occurring also in more exposed localities were particularly well developed.

Taraxacum croceum was frequently codominant with *Sibbaldia procumbens*, and was usually present on the more sheltered banks. On less well-defined banks and at the edges of all banks *Salix herbacea* and *Oxyria digyna* were usually dominant. In many localities *Veronica alpina* was abundant and sometimes codominant although it was absent from all banks in the central part of the island.

Other species of varying importance were:

Polygonum viviparum	a.	Poa pratensis	f. o.
Equisetum arvense	a.	Festuca vivipara	o.
Ranunculus pygmaeus	a.-f.	F. rubra	o.-r.
Saxifraga cernua	f.	Arabis alpina	o.
Carex Bigelovii	f.-o.	Gnaphalium supinum	f. absent
Cerastium cerastioides	f.-o.	Potentilla alpestris	r.-absent

In addition, species common on the surrounding slopes entered into the vegetation, especially on banks with a slight slope. Of such species the following were the most frequent:

Cerastium alpinum
Saxifraga caespitosa
S. tenuis
Luzula confusa
Ranunculus glacialis

The majority of the types of vegetation already described were somewhat indefinite and variable. By contrast the "*Sibbaldia*" bank was a much more constant and distinctive community. In addition to *Sibbaldia procumbens* the following species were usually confined to these localities:

Veronica alpina
Potentilla alpestris
Gnaphalium supinum

(10) *Consolidated hollows in lava fields.* In lava fields, even at an early stage of colonization, where the vegetation consisted mainly of lichens there occurred in consolidated hollows a few vascular plants. The hollows provided more shelter and moisture than the surrounding slopes and a more varied vegetation was in consequence found. The first plants to colonize these hollows were *Oxyria digyna* and *Cerastium alpinum*. In specially moist areas, *Saxifraga rivularis, Poa alpina* and *Festuca vivipara* and less frequently *Ranunculus glacialis* were found.

In more mature lava fields the vegetation of the hollows often showed progressive development towards a rather poor "*Sibbaldia*" bank type. Plants of *Empetrum hermaphroditum* were found in such situations in the south of the island while in one locality the fern *Cystopteris fragilis* occurred.

(11) *Active stone polygon fields.* Polygon fields did not cover a very large area on Jan Mayen. They were absent from the greater part of the central and southern region where the porosity of the underlying lavas was not conducive to their formation. However, on the south face of Beerenberg at the altitude 200–400 m., some fairly extensive polygon fields occurred. The origin and development of these structures have been discussed recently by Polunin (1934) and others.

Varying forms of polygons and stripings were found and any vegetation present was confined to the intervening tracts between the polygons. The following species occurred, usually as rather stunted plants in an open vegetation:

Ranunculus glacialis
Cochlearia ? officinalis
Cerastium alpinum
C. cerastioides
Saxifraga caespitosa
S. tenuis
Saxifraga nivalis
Polygonum viviparum
Oxyria digyna
Luzula ? confusa
Carex ? lagopina
Poa alpina var. vivipara

There was a small development of mosses (*Rhacomitrium* spp.) with occasional foliaceous lichens.

(12) *Stabilized stone polygon fields.* Only one stabilized polygon field was examined in detail. It was situated on the northern flank of Hochstetter Crater. Similar but smaller areas did however occur elsewhere. The polygons were usually large, up to 3 m. in width, and the plants were again mainly in the intervening tracts where belts of closed vegetation developed, the principal species being:

Luzula ? confusa	a.-d.	Cochlearia ? officinalis	o.
Polygonum viviparum	f.-d.	Equisetum arvense	o.
Salix herbacea	a.	Saxifraga tenuis	o.
Oxyria digyna	f.	Sagina ? caespitosa	r.
Ranunculus glacialis	f.	Saxifraga rivularis	r.
Cerastium alpinum	f.	Koenigia islandica	o. (moister places)
Festuca vivipara	f.	Silene acaulis	f. (in exposed parts)
Poa alpina var. vivipara	o.		

On sloping banks between the polygons mosses, principally *Rhacomitrium? canescens*, were dominant though elsewhere they were less abundant.

(13) *Solifluxion areas.* Solifluxion areas were of more frequent occurrence than the polygon formations described above. They were typical of many of the moister slopes and took the form of small irregular terraces of more or less flat soil or gravel. Plants were rare on the terraces but the gently sloping banks between them bore a varied vegetation in which bryophyta of the following species were generally dominant:

Rhacomitrium lanuginosum R. canescens	the dominant species	Bryum sp.
Dicranoweisia crispula		Aulacomnium turgidum

Lichens were of common occurrence, especially *Cetraria islandica* and *Stereocaulon denudatum* (often the var. *umbratum*). There were also present a number of vascular plants, viz.:

Salix herbacea	a.-s.d. (rarely d.)	Saxifraga tenuis	f.
Equisetum arvense	f.-s.d. (absent in drier regions)	S. nivalis	f.
		Ranunculus glacialis	f.
Polygonum viviparum	a.	R. pygmaeus	f.-o. (moister places)
Cerastium alpinum	a.	Silene acaulis	o.
Oxyria digyna	a.	Minuartia biflora	o.
Saxifraga caespitosa	f.	Sagina nivalis	o.
Luzula confusa	f.	Poa alpina var. vivipara	r.-o.
Carex ? lagopina	f.	Festuca vivipara	r.-o.

In addition, *Epilobium alpinum* was found on one slope in Fishburn Valley while *Euphrasia frigida* (probably the var. *pusilla*) occurred on the surface of the terraces in several parts of the district.

(14) *Moist earth slides.* On the moist slopes already described (type 4) there were occasionally small areas where denudation had taken place, presumably by the action of snow, and bare tracts of moist soil were exposed. Areas of this type were rare since, owing to the thin layer of soil on the majority of slopes, denudation more commonly resulted in the formation of screes. In Fishburn Valley, however, several moist earth slides were found. In these situations there was an abundant supply of moisture and the first colonizers were *Cerastium alpinum* and *Saxifraga caespitosa.* These species were followed by *Saxifraga nivalis, Carex lagopina, Poa pratensis* and *P. alpina* var. *vivipara.*

(15) *Screes and moraine slopes.* On screes and moraine slopes as yet incompletely stabilized *Ranunculus glacialis, Oxyria digyna* and *Cerastium alpinum* were usually the first plants to develop. The survival of the plants depended on the presence of sufficient finely divided material to hold moisture. In these situations the root systems of *Ranunculus glacialis* especially were more extensive than those of individuals growing on stable ground. Other plants which appeared at an early stage were *Saxifraga caespitosa, Salix herbacea* (small plants), *Polygonum viviparum, Silene acaulis, Luzula confusa* and *Poa alpina* var. *vivipara.*

(16) "*Late snow*" *areas.* In many localities a factor of major importance in the development of the vegetation was the time of snow melting. When the present investigations were started (10 July) comparatively few areas at low altitudes remained covered with snow. Observations on these "late snow" areas were consequently limited. The areas examined were floristically similar to comparable regions where the snow had retreated at a much earlier date. No species were confined to the "late snow" areas although *Saxifraga foliolosa* and *Cerastium cerastioides* were especially abundant in such situations. Three types of late snow area will be described here to show the general effects of the snow covering on plant development. Certain of the physiological aspects of the problem will be examined in another communication.

(*a*) On one of the sheltered "*Sibbaldia*" banks in the Fishburn Valley the snow did not melt till the first half of July. Nevertheless, when the bank was examined on 22 July the plants were developing rapidly, the most advanced species being *Taraxacum croceum* and *Ranunculus pygmaeus*, followed in order by *Oxyria digyna, Sibbaldia procumbens* and *Arabis alpina.* In addition *Salix herbacea* had started to throw out new shoots but the mosses were still predominantly brown. The seeds of *Taraxacum croceum* from the previous year were not yet dispersed, showing that in some if not in all seasons the fruits of this species do not reach maturity before the autumn snows commence. Floristically this region resembled banks from which the snow covering had retreated much earlier in the year.

(*b*) At the altitude of about 100 m. on the east of Fishburn Valley there was a snow patch of considerable size which persisted throughout the visit of the authors. It was examined first on 16 July. At the lower margin of the snow patch leaves of *Taraxacum croceum* and *Polygonum viviparum* were found growing up through 2–4 cm. of snow. *Taraxacum* leaves were chlorotic while those of *Polygonum* were brown and translucent. Green leaves of *Sibbaldia procumbens* were also found, but in no case had they pierced the surface. The light intensity was reduced to a third by the snow covering. In another part of the same patch where the depth of snow was 50 cm., the lower 5–10 cm. being hard ice, a number of species were found to have put out new leaves, viz. *Saxifraga ?tenuis*, *Taraxacum croceum*, *Arabis alpina* and *Oxyria digyna*, together with a grass too small for identification and other unidentified seedlings. All but *Taraxacum croceum* possessed normal green leaves. The light intensity was here reduced to 2 % of daylight. The soil temperature was 0° C. but the soil was not frozen. It appears that plants commence to develop as soon as melt water from the melting of snow higher up the slope percolates down beneath the snow covering.

To gain some idea of the rapidity with which the vegetation developed after the retreat of the snow a line of cairns was made along the edge of the retreating snow. Within three weeks of the snow melting plants had developed and flowered. The plants were well grown and by comparison with those in other regions it appeared that almost their full complement of leaves had been already formed. Floristically the only point of note was the abundance of *Cerastium cerastioides* which was markedly more common than in regions from which the snow had retreated earlier.

(*c*) Especially on the Wildberg several small hollows were seen in which snow persisted late in the season. These differed from the other types described above in that drainage was slow owing to the concavity of the ground. Thus during the melting of the snow swampy conditions prevailed. *Koenigia islandica* and other plants typical of wet regions (type 8) occurred, *Saxifraga foliolosa* being particularly characteristic of these regions.

(17) *Alluvial gravel beds.* Depending on the abundance of water supply and its constancy during the summer two types of vegetation developed on alluvial gravel beds:

(*a*) Constantly moist beds with the water table close to the surface were found where streams entered lagoons. The porous nature of the soil which has been stressed already caused a great part of the drainage to be underground and as a result beds of this type were comparatively rare. In the areas examined the water table was only 5–15 cm. below the surface even in dry weather in August, and earlier in the summer it is probably practically on the surface. The vegetation was open and the majority of the plants were small, the following being the main species present:

Cochlearia groenlandica	a.-d.	**Saxifraga caespitosa**	o.
Koenigia islandica	a.-d.	**S. nivalis**	o.
Ranunculus glacialis	o.-a.	**S. tenuis**	o.
Cerastium cerastioides	f.	**Salix herbacea**	o.
Oxyria digyna	f.	**Festuca vivipara**	o.
Catabrosa algida	f.		

Moss (?*Bryum* sp.) was fairly common, but did not form a continuous carpet.

Wide variations between localities were noticed. The frequencies stated here were observed on the delta of Tornoe River, North Lagoon which was a characteristic area. The plants of *Koenigia islandica* in this region were of a vivid red colour in contrast to the typical green plants growing in wet moss beside streams. It is not unlikely that the coloration was due to nutrient deficiency and this question is under investigation.

(*b*) The conditions of beds in melt-water valleys were in many essential respects different from those described above. Only in spring when the winter snows were melting was the supply of water abundant. In the late summer the water table was a considerable distance below the surface, and the upper layers of gravel were extremely dry. Beds of this type occurred in several valleys. *Ranunculus glacialis* was usually the most common, sometimes the only plant present. The individuals were deep rooted and spaced 50 cm. or more apart. Other plants occasionally found were *Oxyria digyna*, *Cochlearia groenlandica*, *Sagina nivalis*, *Cerastium alpinum*, *Festuca vivipara* and *Poa alpina* var. *vivipara*, the last-named species being in somewhat moister places. It may be noted that, in a number of localities, vegetation of the *Sibbaldia* bank type was well developed in the more moist and sheltered hollows where the gravel beds abutted on the neighbouring slopes.

(18) *Steam vent.* On the summit of Egg Bluff, a particularly exposed locality, there was a small steam vent, the only remaining sign of volcanic activity on the island. The surrounding ash was for a considerable distance barren of vegetation except at the margin of the vent itself where a very stunted development of *Bryum argentum* was found.

C. *Types controlled by biotic factors*

There remain for consideration under this heading the various types of vegetation which developed in localities especially enriched by the droppings of birds or mammals. Sea birds in large numbers were found almost everywhere on the coastal cliffs, the most common species being fulmar petrels, Brunnich guillemots, puffins, glaucous and kittiwake gulls and little auks. The vegetation both on the faces of the bird cliffs and on the slopes beneath was characteristically more luxuriant than in other situations. A similar effect, though less widespread, was seen in the neighbourhood of the burrows of arctic foxes—the only mammals found on the island. Although Jan Mayen has never supported a permanent population there was one small area in which the vegetation had been modified as a result of human agency and it is appropriate for consideration here.

For purposes of description it is convenient to classify the vegetation controlled by the above-mentioned factors into four types, viz.:

(19) Faces of bird cliffs. (20) Slopes below bird cliffs.
(21) Fox burrows. (22) Human habitation.

(19) *Faces of bird cliffs.* A luxuriant vegetation occurred on the faces of coastal cliffs frequented by sea birds where the rocks are sufficiently weathered for plants to take root and where there was an adequate supply of moisture. *Cochlearia ?officinalis* was almost always the dominant plant and grew with great luxuriance even on very steep faces where also *Saxifraga rivularis* was usually abundant and sometimes dominant or codominant especially in moister places. Other species were:

Poa alpina var. vivipara	o.-f.-(very occasionally cd.)	Catabrosa algida	o.
Oxyria digyna	f.		

The vegetation showed remarkably little variation from one locality to another and it was rare for vascular plants other than those cited to be present. Hygrophylous mosses (?*Hypnum* spp.) occurred but did not play an important part in most localities. Occasionally the liverwort *Marchantia polymorpha* was found in moist places under the shelter of *Cochlearia officinalis.*

This vegetation was typical of cliffs on almost every part of the coast. Occasionally, however, drier and less-weathered cliff faces were seen. In such situations the vegetation was confined to ledges and was made up of a number of the smaller plants which are a feature of open rocky ground.

(20) *Slopes below bird cliffs.* The slopes below bird cliffs frequently bore a more varied vegetation than the faces of the cliffs. Wide variation in both the floristic composition and the density of the vegetation occurred, dependent upon the nature and stability of the soil, the water supply, shelter from winds and the amount of bird droppings. The moist and dry localities will be considered separately.

(*a*) *Moist localities.* Regions of this type were comparatively rare as in most places the porosity of the broken rocks underlying the slopes caused rapid drainage. At The Pillar (Saule)[1] and Cape Traill, however, a particularly large development of soil of greater water-holding capacity provided a more constant and abundant water supply. A few smaller areas of this type were also seen. These localities were characterized by the abundance of *grasses* which were here dominant although in other situations they rarely played an important part in the vegetation. The main species were:

Festuca vivipara	d.	Poa alpina var. vivipara	o.-a.
Poa pratensis	a.		

Other characteristic plants were:

Oxyria digyna	a.-cd. occ.d.	Draba arctica	o.-f.
Cochlearia groenlandica	f.	Taraxacum croceum	f. (more sheltered situations)
Saxifraga caespitosa	f.	Salix herbacea	f.-d. (exposed places)
S. tenuis	f.	Cerastium alpinum	o.

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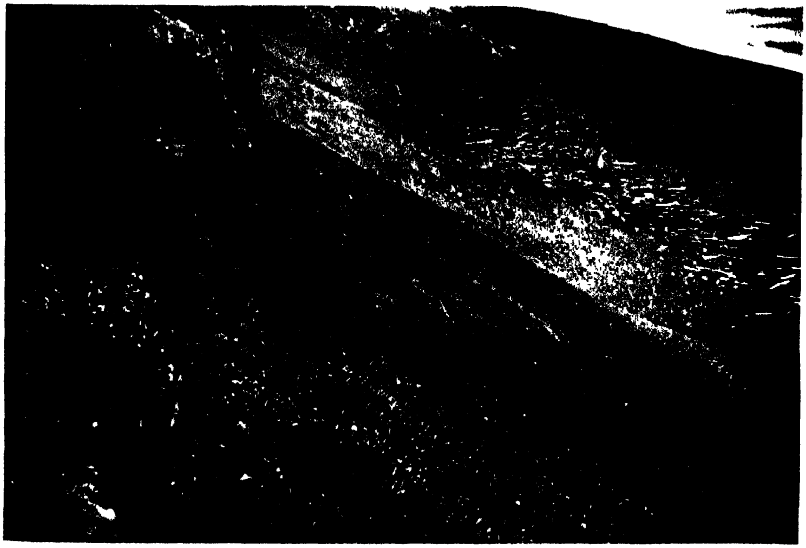
[1] The Pillar is a coarse agglomerate core on the shore of the South Lagoon. Although it is, geologically speaking, dissimilar to the coastal cliffs the presence of large numbers of sea birds makes it appropriate for consideration under the present heading.

Phot. D. F. Ashby

Phot. 3. "Volcanic Desert", Jameson Bay, Jan Mayen Island.



Phot. D. Westwood

Phot. 4. Bird cliff vegetation (Fishburn Bay, Jan Mayen Island) consisting of a luxuriant community of *Oxyria digyna* and *Taraxacum croceum* at the cliff foot, drift wood on beach below.

In addition to these species several others occasionally appeared but were not typical of such localities. Mosses were infrequent except in the more exposed situations.

(*b*) *Drier localities.* The majority of the slopes below bird cliffs were comparatively dry. On the larger slopes a marked zonation of the vegetation was found, while the vegetation became less luxuriant on the lower parts of the slopes further from the cliffs. This zonation was particularly well shown below a small bird cliff in Fishburn Bay, and a special study of this area was made to investigate the correlation between the vegetation and the nitrogen level in the soil. The zonation is indicated diagrammatically in Fig. 2. The slope fell about 100 m. and was about 300 m. long. While it showed a more clearly marked zonation than was found elsewhere, the various types of vegetation were of wide occurrence, and it differed from other localities mainly in its uniform and unbroken character.

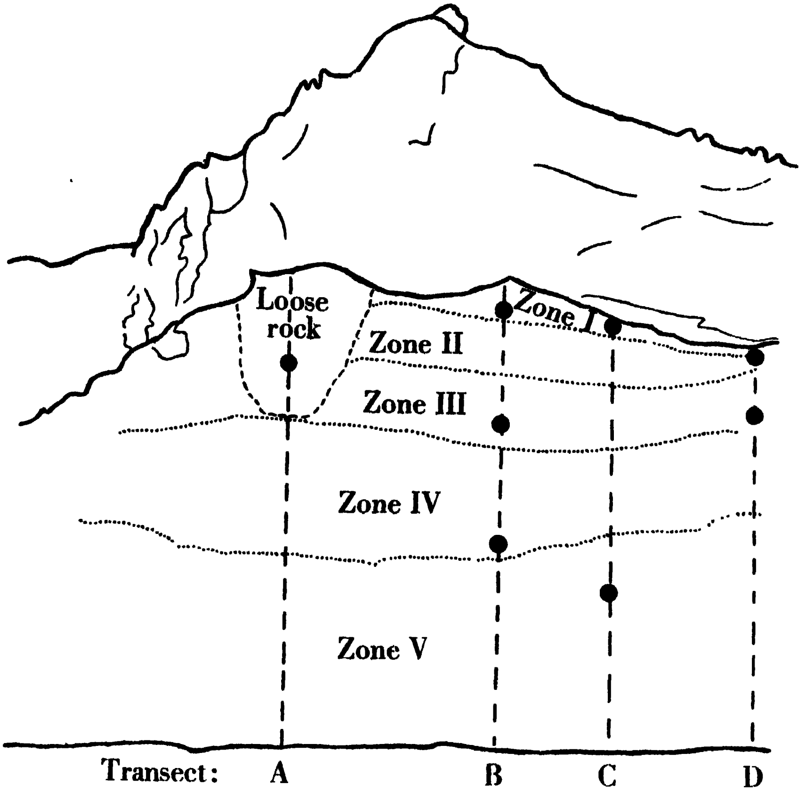


Fig. 2. Diagram of Fishburn bird-cliff area showing the zonation of the vegetation.

The vegetation was mapped by taking transects down the slope. Transect A (Fig. 2) on the left-hand side of the slope lay chiefly in a region of loose unstable rock debris of apparently recent origin. Transects B and C were centrally placed on the slope, while transect D was towards the right-hand edge of the region. At the points indicated in Fig. 2 soil samples were taken for analytical, protozoological and bacteriological investigation; the results of this work will, however, be discussed in a subsequent paper.

Some brief remarks on the nature of the soil will however not be out of place here. The upper part of the slope consisted of well-weathered volcanic tuffs to a depth of about 10 cm., was rich in organic matter and there were few exposed rocks. Lower down the richness of the soil decreased and the surface became more stony, while towards the bottom of the slope the surface layers were composed almost entirely of sand. High-water mark was within a few metres of the foot of the slope.

Zone I. This zone, up to 8 m. in width, was situated immediately at the foot of the cliff and consisted of a closed association of *Oxyria digyna* and *Taraxacum croceum* (Pl. 11, phot. 4). Adjacent to the cliff *Oxyria digyna* was dominant while further out *Taraxacum croceum* became increasingly important. Other species were absent. On the right-hand side of the slope this zone merged into zone II.

Zone II. The second zone, 5–10 m. deep, was characterized by the appearance of several grasses, especially *Poa alpina* var. *vivipara. Taraxacum croceum* and *Oxyria digyna* became decreasingly important with increasing distance from the cliff face, but in the upper part of the zone *Taraxacum* was dominant or codominant. Other species present were:

Festuca vivipara	f.	Polygonum viviparum	o.-f.
F. rubra	f.	Saxifraga nivalis	o.
Trisetum spicatum	o.	Silene acaulis	o.-f.
Poa glauca	o.	Cerastium alpinum	o.-f.
Arabis alpina	o.	Cochlearia sp.	o.

Polygonum viviparum, Silene acaulis and *Cerastium alpinum* were more common on the lower part of the zone. Mosses were rare.

Zone III. In this band, from 20–30 m. in width, the salient feature was the presence of *Salix herbacea* associated with mosses, mainly *Rhacomitrium canescens*. Towards the right-hand side of the slope *Salix herbacea* was dominant; elsewhere it was codominant with *Rhacomitrium*, other species being:

Polygonum viviparum	a.	Draba nivalis
Cerastium alpinum	a.	Sibbaldia procumbens
Silene acaulis	a. (large clumps)	Saxifraga caespitosa
Draba arctica		Luzula sp.

Grasses of the species found in zone II were occasionally present. In the lower part of the zone patches of bare ground appeared and the smaller plants became less common. From here downwards the vegetation became progressively more sparse and the amount of bare ground increased steadily. It may be noted that this was the only locality where *Sibbaldia procumbens* was found in such an exposed situation.

Zone IV. This zone which varied in width from 20 to 40 m. was characterized by the appearance of *Halianthus peploides* and by the increasingly sandy nature of the soil. Other plants which appeared for the first time were:

Carex incurva (a sand binder)
Ranunculus glacialis
Martensia maritima

Of the species found also on the upper zones *Silene acaulis* was the most common, though stunted plants of *Oxyria digyna* and less frequently of other species occurred infrequently. Towards the lower margin of the zone all other plants were subordinate to *Halianthus peploides.*

Zone V. In the lowest zone, stretching down almost to high-water mark, the vegetation consisted of occasional clumps of *Halianthus peploides* with, less frequently, *Martensia maritima.* Especially in the lower part of the zone the plants were spaced widely apart.

(21) *Fox burrows.* By the burrows of arctic foxes small patches of luxuriant vegetation were commonly found. *Poa alpina* var. *vivipara* and *Taraxacum croceum* are in many places the dominant species.

Special mention must be made of an area about 5 m. square on the hillside behind Hope Bay. Here, under fallen basalt blocks, were an unusually large number of fox burrows. Many bones and droppings lay on the ground and there was a strong and characteristic odour. The soil, much darker than that of the surrounding slope, was rich in organic matter and there was a luxuriant vegetation of a type not found elsewhere on the island. *Alchemilla* sp. (closely allied to *A. glomerulans*) was dominant and was confined to this area. Other species were:

Potentilla alpestris
Sibbaldia procumbens
Gnaphalium supinum
Veronica alpina

At the mouth of one burrow grew a single plant of *Cystopteris fragilis.*

The occurrence of this luxuriant vegetation on a hillside elsewhere supporting only the normal hillside type was most striking. It should be emphasized that the situation was not sheltered to a particularly great degree, neither was the water supply better than in many other localities. Thus there can be no doubt that the conditions which permitted the development of this special vegetation were directly due to the foxes.

(22) *Human habitation.* The last type of vegetation remaining to be described is that which was modified as a result of human habitation. The only locality of this type was in Wilczec Valley, behind Mary Muss Bay, where the base of the Austrian Polar Year Expedition of 1882–3 was situated. This locality is of interest not only on account of the fact that nowhere else was the vegetation affected by human agency but also because it demonstrates most clearly the effect of increased soil nutrients on the vegetation.

Except immediately surrounding and below the ruins of the station there was a very scanty development of vegetation, and the soil was sandy and unstable. Close to the station however there was a dense vegetation dominated by *Oxyria digyna* almost to the exclusion of other plants, though *Poa alpina* var. *vivipara* and *Cerastium alpinum* occurred occasionally and there was a small development of moss (? *Rhacomitrium* sp.).

It may be mentioned that although whaling bases were established in the seventeenth century on several parts of the coast, and especially at Walrus Gat, there is at present no indication of the vegetation having been modified. Apparently any enrichment of the soil which may have occurred has been lost with the passage of time, probably as a result of leaching.

DISCUSSION

In the foregoing description of the vegetation of Jan Mayen an attempt has been made to emphasize the way in which the various climatic and edaphic factors determine the variations in the type of vegetation observed from place to place. In this connexion shelter, the time of snow retreat, water supply and the available mineral nutrients are believed to be the most important factors. It may be pointed out that, since comparatively small differences in temperature occur from one locality to another on the island,[1] except at high altitudes, temperature is to only a small extent responsible for the differentiation of the various plant communities within the area. In the present discussion certain general conclusions as to the effects of the environmental factors will be advanced and preliminary observations will be made on the successional relationships of the vegetation. The supply of soil nutrients and the general effects of the arctic environment on plant growth will however be reserved for consideration in later papers.

Shelter from wind. Attention has already been directed to the high prevailing winds which characterize the climate of Jan Mayen (Table 1) and thus the degree of shelter from wind in any one locality is of especial importance in determining the type of vegetation which develops. In an arctic environment shelter from wind serves two roles. Not only are the plants protected from the effects of wind during the growing season but also at the commencement of winter they are more rapidly covered by snow and they remain so until a late date in the spring. In exposed situations fallen snow tends to be blown away, while on the other hand drifts accumulate in the more sheltered places.

The effect of wind in retarding plant growth is well known. Kreutz (1938) found that the growth of cabbages was increased 300% by sheltering them from strong winds. It was evident from the general facies of the Jan Mayen vegetation that the wind factor was operative—plants growing in sheltered places were strikingly larger than individuals of the same species in exposed localities.

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[1] There appears however to be evidence of considerable temperature gradients within small areas in other arctic regions.

At Fishburn where a camp was maintained throughout the summer it was noticeable in mid-August that plants of *Oxyria digyna* growing under the lea of a stone wall built a month earlier, were much larger than plants not so sheltered. No quantitative measure of the effect of wind on growth was however possible and it must be borne in mind that factors other than shelter are usually operative also. It will be shown in a later paper that a higher nitrogen supply usually prevails in sheltered localities, thus the greater density of the vegetation in such situations is correlated with the more favourable nutrient supply as well as the shelter from wind.

The effect of snow covering. Observations on the effect of snow covering were restricted by the fact that the field work was carried out entirely in the summer. It has been mentioned already that only in small areas was snow still lying when the expedition reached the island and this discussion is therefore necessarily somewhat generalized. Two types of snow effect may be distinguished, (i) the protective effect of the covering in winter, (ii) mechanical injury due to snow movement; the former is of especial importance. Böcker (1933) in his studies of the vegetation of East Greenland has emphasized the importance of snow cover and has classified the plant communities into three groups in terms of the length of time during which the snow persists. A thick covering in winter is a protection against extreme cold and the desiccation which may occur when living tissue is exposed to air at very low temperatures (see Lundegårdh, 1931, p. 85). Thus in the localities where the covering is not complete till late in the winter and is most rapidly removed in spring the vegetation suffers. At the other extreme are situations where the snow lies late into the growing season and the growing period is consequently curtailed. This may result in the seasonal development not being complete when the winter snows commence, as was seen on certain "late snow" areas where *Taraxacum croceum* seeds were, in the following spring, still not disseminated. It would appear that, on Jan Mayen, the optimum duration of snow covering occurred on "*Sibbaldia*" banks facing south.

Mechanical damage resulting from snow movement was found on some exposed slopes but it was of comparatively localized occurrence.

Water supply. It has been emphasized that despite the generally humid atmosphere on Jan Mayen, water shortage restricted the development of vegetation in many localities. This situation resulted from the porous nature of the underlying rocks as well as from the thin layer of soil generally low in humus and consequently of low water holding capacity. In the drier localities mosses (especially *Rhacomitrium* spp.) were usually the dominant plants though such species as *Salix herbacea*, *Empetrum hermaphroditum* and *Draba* spp. could survive considerable water shortage. Closed communities of vascular plants were confined to the moister localities.

Succession

In discussing the successional relationships of the Jan Mayen vegetation no attempt will be made to present a detailed schema. It is possible, however, to indicate a general successional trend. Plant colonization occurred on three main types of igneous substratum—namely, lava flows, volcanic tuffs and similar rocks, and ash derived from dust eruptions. In areas, usually more restricted, vegetation was found on eroded material, either marine sand, moraine or alluvial flats. The relationships between the communities developing in these various types of regions will be indicated briefly.

An early stage in the development of vegetation on lava flows has been described (type 1). Crustaceous and foliaceous lichens were the first colonizers, while on more mature fields the dry moss communities (type 2) marked the next stage in development; here a number of vascular plants, especially *Salix herbacea*, were found. On the south-western side of the island the wet moss communities (type 3) resulted, it is believed, from climatic causes. Except in localized areas where special physiographic features provided unusually favourable conditions for plant growth the moss communities represented the final stage in the development of the vegetation. On the other hand "*Sibbaldia*" banks (type 9) were found in small sheltered places while, beside streams, communities of vascular plants (type 8) also occurred.

On volcanic tuffs no very early stages in plant colonization were found. The greater depth of soil resulting from the weathering of the rocks and their less porous nature permitted more luxuriant plant growth but the successional stages appeared to be parallel to those on lava fields, the "*Sibbaldia*" bank type being in both cases the climax in sheltered situations.

Little need be said here of the development of the meagre plant covering found on volcanic ash as it has already been described (type 6). The entire absence of lichens and mosses during the early developmental stages was in contrast to the situation found on the other types of igneous material.

Coastal sand was colonized first by *Halianthus peploides*, often the only plant present, while on alluvial gravel beds where the water-table was sufficiently near the surface a rather sparse, though floristically varied, vegetation of vascular plants developed. On consolidated moraines or other broken rock, crustaceous lichens were the first plants to appear and were followed by mosses (especially *Rhacomitrium*) and foliaceous lichens which in turn gave place to *Salix herbacea* or *Empetrum hermaphroditum*. Finally, attention must be drawn to the very marked effect of animal droppings on vegetational development (see types 18–22).

SUMMARY

1. The programme of botanical work undertaken on the Imperial College Expedition to Jan Mayen has been outlined and the geography and climate of the island summarized.

2. The vascular flora of the island is small, comprising so far as is known only 58 species of vascular plants. Over the greater part of the island the vegetation was dominated by mosses or lichens. In limited areas, however, specially favourable conditions permitted the development of closed communities of vascular plants.

3. For purposes of classification the vegetation of the island has been divided into 22 types defined both on the basis of floristic content and the environmental conditions.

4. These communities have been described, together with the conditions necessary for their development.

5. It is concluded that the degree of exposure to wind, nitrogen and water supply and the time of snow retreat are the major factors which determine the distribution of the various types of vegetation.

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SOIL TEMPERATURES DURING FOREST FIRES AND THEIR EFFECT ON THE SURVIVAL OF VEGETATION

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(*With Plate* 12 *and six Figures in the Text*)

I. Introduction

Although some attention has been directed to soil temperatures in deserts (Buxton, 1924), the temperature of the soil during forest fires has received little consideration. The only work on this subject is that of Heyward (1938), who measured the temperature of the soil during the burning of grassland. The occurrence of a fire and the resulting high soil temperatures are important with regard to the death or survival of seeds or other plant organs, while the artificial burning of cultivated grassland, such as stubble, increases the soil temperature and may cause the death of micro-organisms.

In the following account, a practicable and simple method for measuring soil temperature is described, and data are given showing the temperatures at various depths below the surface in wet and dry soils. The survival of the vegetation is discussed with special reference to lignotubers (Kerr, 1925) and to the resistance of seeds to high temperatures.

II. Soil temperature

A. *Method*

The method employed for measuring soil temperature was as follows: At various depths in the soil, small glass tubes containing organic compounds of known melting-points were buried. The tubes were cut from thin-walled glass tubing of approximately ⅛ in. internal diameter. Each tube was about 2 in. long and was sealed at one end. A small quantity of the crystalline organic compound was introduced, and into the open end of the tube was inserted a small roll of paper. The organic compounds used were:

Compound	M.P. (° C.)	Compound	M.P. (° C.)
Menthol	43	Pyrogallol	132
Thymol	50	Phenacetin	135
p-Anisidine	57	Benzoin	137
β-Brom-naphthalene	59	*m*-Nitrobenzoic acid	140
Coumarin	67	Benzilic acid	150
2:4-Dinitrotoluene	70	Salicylic acid	156
Vanillin	81	*p*-Amino-acetanilide	162
m-Dinitrobenzene	90	Camphor	175
α-Naphthol	95	Succinic acid	180
o-Toluic acid	105	*m*-Hydroxybenzoic acid	200
m-Toluic acid	109	Anthracene	213
β-Naphthylamine	111	Phthalimide	233
p-Nitrophenol	114	Anthraquinone	250
Benzoic acid	122		(sublimes)

The prepared tubes were placed in flat tins (3½ × 2 × ¾ in.) which were buried in the soil.

In order to maintain, as far as possible, natural soil conditions, a deep hole was dug and small holes were scooped horizontally at various depths. The tins, containing the tubes, were filled with soil and inserted into the smaller holes horizontally so that the column of soil above the tubes was untouched. Temperatures below 43° C. were recorded by means of mercury thermometers pushed horizontally into the soil below the batteries of tubes. The cavities around the tins were packed tightly with soil and the soil from the large hole was replaced in approximately the same position from which it was removed. Fires were then lit on top, the diameter of each fire being about 2 ft., with the centre as near as possible above the tubes. After the fires had burned out, the tubes were recovered. The soil temperatures at the various depths were recorded by the melting of some of the organic compounds.

This method, though not as accurate as measurement with thermocouples (Heyward, 1938), has one advantage, namely, that the organic compounds will not melt after a momentary exposure, but require a temperature at or above the melting-point for some little time. Therefore their behaviour supplies more reliable information as to the effect of fire on plants.

B. *Results*

(*a*) *Soil temperatures during natural fires.*

Although fires are frequent in the *Eucalyptus* forests of Australia, trees are rarely burned out, and most of the fuel is supplied by the undergrowth. Consequently a fire was lit in a forest area which was known not to have been burned during the last six years. No extra fuel was added. The fire was allowed to burn out naturally; this required ¾ hr.

The soil temperature at a depth of 1 in. and that at the surface are given in Table 1. The surface temperature was obtained by pressing "melting-point tubes" horizontally into the soil so that the upper surface of the glass was just exposed.

Since fires in this district cross an area rapidly and do not burn for any length of time in the same place, these figures represent the probable temperatures during fire on the Hawkesbury Sandstone in the Sydney district.[1]

The temperatures recorded, though high at the surface, are surprisingly low at a depth of 1 in. The wide variation between the individual readings can be attributed to the varying amounts of dead plant material lying on the surface.

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[1] The Hawkesbury Sandstone formation has a wide exposure in the central coastal district of New South Wales. It is Triassic in origin and "consists mainly of massive sandstones and grits, which attain a maximum thickness of 1100 ft. at Sydney" (Süssmilch, 1914).

(*b*) *Probable maximal temperatures during fire.*

In order to estimate the probable maximal temperatures during fire, the equivalent (as dead fuel) of the vegetation (excluding trees) from a quadrat of 9 sq. ft. was built into a pile (diameter about 2 ft.) and lit. The fire burned for 2 hr. Such a fire will represent the probable maximal intensity, assuming that the whole of the vegetation is burned.

Batteries of tubes were buried at depths of 1 and 3 in. and thermometers

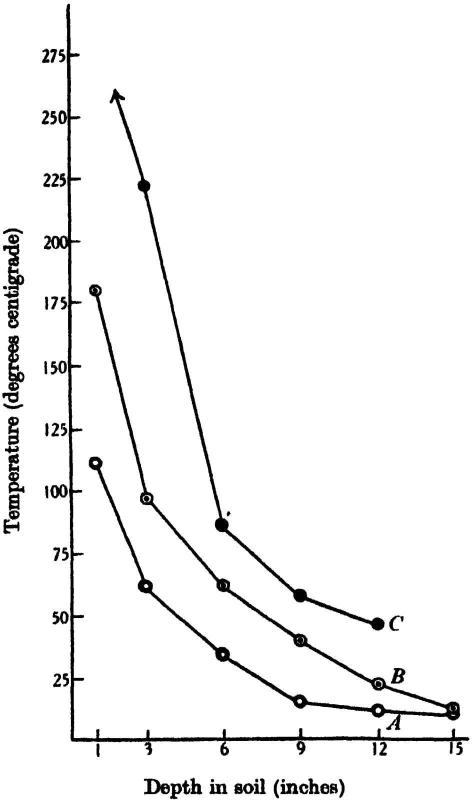


Fig. 1. Soil temperature during fire plotted against depth in the soil. *A*, probable maximal temperatures during fire (trees not burned); *B*, mean maximal temperatures if trees are burned, fire burning for 2 hr.; *C*, temperatures in extreme case, fire burning for 8 hr.

Table 1. *Temperatures at the surface and at a depth of* 1 *in. during a forest fire under natural conditions*

Depth	Temperature (° C.)					
Sample ...	1	2	3	4	5	6
Surface	111–114	175–180	200–213	135–140	81–90	132–135
1 in.	<43	57– 59	59– 67	43– 50	<43	43– 50

at 6, 9 and 12 in. below the fire. The results obtained are shown in Table 2 and are summarized graphically in curve *A*, Fig. 1. The surface temperature exceeded 250° C. At a depth of 1 in. the temperature was 114–122° C., while at 3 in. a temperature of 50–59° C. was recorded. Below this level, the temperature was not sufficiently high for a long enough period to harm any plant organ.

Table 2. *Probable maximal soil temperature at various depths below the surface. "T" after a temperature indicates that this temperature was measured with a thermometer*

Depth (in.)	Temp. (° C.)
Surface	>250
1	111–114
3	59–67
6	35 T
9	15 T
12	12 T
15	11 T

(*c*) *Maximal temperatures if trees are burned.*

To ascertain the highest temperature that could occur if the whole of the vegetation, including trees, were completely burned, the following method for estimating the amount of fuel was adopted: the number of trees in 100 sq. yd. was counted and the amount of fuel contained in them was roughly estimated. One-hundredth part of this amount of dry timber was collected and piled into a heap of 2 ft. diameter, together with fuel to account for the undergrowth, on a piece of land in which were buried batteries of tubes.

The temperatures obtained under these conditions are given in Table 3, column 2 and are represented graphically in Fig. 1, curve *B*. The temperature at a depth of 1 in. was 175–180° C., while at 9 in. the temperature exceeded 40° C.

Table 3. *Maximal soil temperature*

	Temp. (° C.)	
Depth (in.)	Fire burning for 2 hr.	Fire burning for 8 hr.
1	175–180	>250
3	95–105	213–233
6	59– 67	81– 90
9	40 T	57– 59
12	22 T	43– 50
15	13 T	—

The results obtained from this fire represent the mean maximal temperatures in a forest, i.e. if the whole of the fuel during the fire were distributed equally over the area.

Quite frequently, however, fallen trees or large stumps may burn for hours or even days. Therefore to gain some idea of the maximal temperature in such an extreme case, a fire, burning fuel at approximately the same rate as the one described above, was stoked for 8 hr. The results are given in Table 3, column 3, and Fig. 1, curve *C*.

These figures show that with long periods of time, the soil is appreciably heated to a depth of 1 ft., while at a depth of 1 in. the temperature exceeded 250° C. Thus the surface temperature, by extrapolation, would lie in the vicinity of 450° C.

The curves plotted in Fig. 1 were obtained from fires lit within 8 ft. of each other on a piece of land which showed fairly uniform water content and texture.

(*d*) *The effect of water content on soil temperature.*

Since the specific heat of sand is as low as 0·2, it is obvious that the specific heat of soil will depend largely on the water content. To illustrate this point, two fires were lit, one on a wet and the other on a dry soil. The water content of the soil before the fire is shown in Fig. 2, curves *A* and *B* respectively. The amount of fuel used for each fire was 20 lb. of *Eucalyptus* wood, cut from the same tree and piled on to an area of approximately 4 sq. ft. The fires were allowed to burn to embers, the time in both cases being 1½ hr.

The results are shown in Table 4 and Fig. 3. From these data it can be seen that the water content of the soil influences the temperature during fire, a high water content causing a retardation in the conduction of heat.

Table 4. *Soil temperature in wet and dry soils*

	Temp. (° C.)	
Depth (in.)	"Wet" soil	"Dry" soil
1	132–135	>250
2	95–105	109–111
4	57– 59	90– 95
6	34 T	57– 59
8	26 T	43– 50
10	22 T	29 T
12	20 T	20 T

It is noteworthy that the water lost by evaporation diffuses into the atmosphere and does not pass downwards and condense, since the percentage of water in the soil at lower levels does not increase after fire (Fig. 2, curves *C* and *D*).

(*e*) *The effect of high temperatures on the physical properties of the soil.*

It is usually considered that the effect of fire is to reduce the amount of organic matter in the soil and thereby reduce the water-retaining capacity. The Hawkesbury Sandstone soils, having as a rule a low percentage loss on ignition, are not affected to any great extent by fire. Table 5 gives the physical properties of some soils before and after fire. From these figures it can be seen that fire does not appreciably alter the water-retaining capacity, loss on ignition or *p*H value.

Variations in sampling were avoided in the following manner: small fires were lit and soil samples were collected before and immediately after the fire, the second sample being collected beside the hole left after the first sample was removed. No plant ash or charcoal was included. The amount of fuel used in each fire was the same as that described in § (*b*).

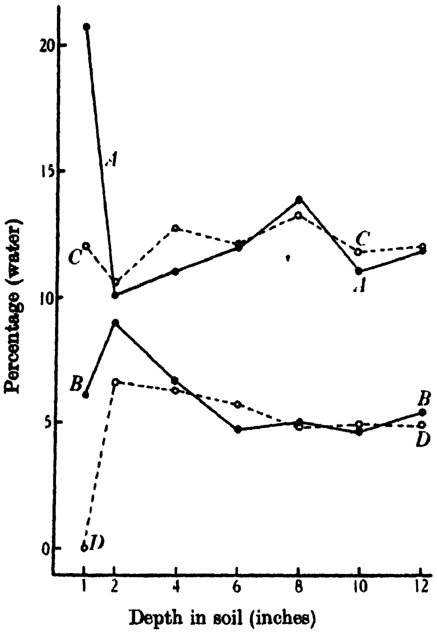


Fig. 2.

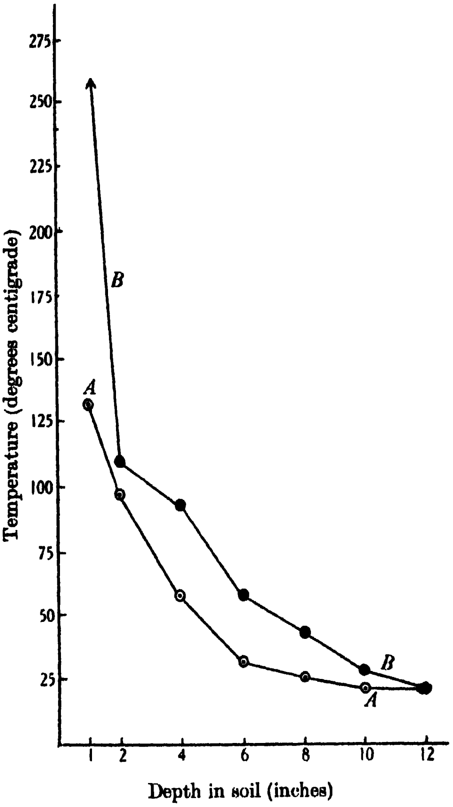


Fig. 3.

Fig. 2. Water content of the soil before and after fire, plotted against depth in soil. *A*, "wet" soil before fire; *B*, "dry" soil before fire; *C*, "wet" soil after fire; *D*, "dry" soil after fire.
Fig. 3. Soil temperature during fire plotted against depth in soil. *A*, "wet" soil; *B*, "dry" soil.

Table 5. *Physical properties of soil before and after fire*

	*p*H		Water-retaining capacity		% Loss on ignition	
Community	Unburned	Burned	Unburned	Burned	Unburned	Burned
Dry scrub	5·0	5·0	44	38	7·6	4·4
	4·7	4·5	48	42	12·8	8·6
Eucalyptus forest	5·4	5·0	32	29	2·9	2·7
	5·1	5·0	31	29	3·1	2·9
Moist scrub	5·2	4·8	31	28	1·8	1·8
	5·1	4·6	38	30	3·3	2·6
Moss mat	4·9	4·9	40	38	7·1	7·0
	4·6	4·6	56	55	4·9	5·1

C. *Discussion*

If the soil were quite dry and were a homogeneous system, the relationship between temperature and depth would be exponential. But the agreement with an exponential relationship is not close for two reasons: (1) there is a heterogeneous distribution of water in the soil, and (2) at a temperature above 100° C. heat would be utilized to overcome the latent heat of vaporization of water. Therefore there is an unconformity in the curve at this point.

The result of the application of a source of heat at the surface is the desiccation of the surface layers of the soil, so that the system becomes heterogeneous, consisting of an upper dry zone with a relatively high conductivity and a lower zone with a higher water content and therefore a lower conductivity. The logarithmic curves (Fig. 4) exhibit a steep slope near the surface, indicating a rapid conduction of heat by the desiccated surface layers. The remainder of the logarithmic curves are, in every case, a first approach to a straight line, indicating a homogeneous "wet" system.

III. SURVIVAL OF VEGETATION

The foregoing sections show that considerable temperatures are reached in the soil during fire, especially in dry soil, even at a depth of 6 in. In spite of such unfavourable conditions, it is characteristic of *Eucalyptus* forests that after fire regeneration of woody plants is common and dense mats of seedlings appear from seed which has survived the fire.

A. *Regeneration of woody plants*

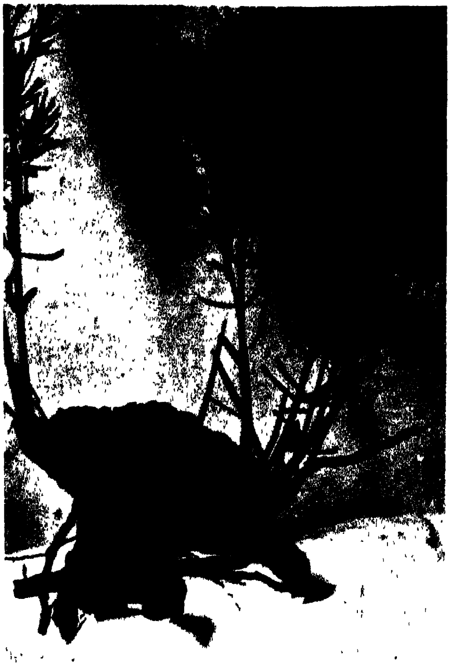
Unlike the forests of the Northern Hemisphere, the *Eucalyptus* forests of Australia are not killed by fire and are therefore capable of regeneration from subaerial and subterranean shoots. The modes of regeneration of woody plants are:

(*a*) Shoots from the trunk and branches (epicormic shoots).
(*b*) Shoots from lignotubers.

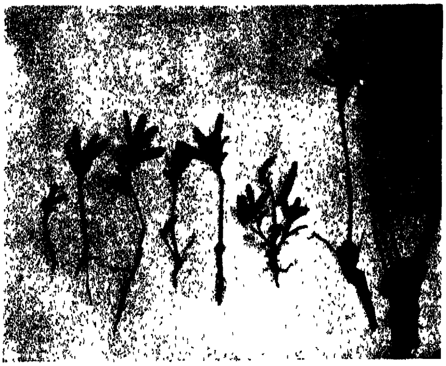
(*a*) Since many Australian trees have a thick bark and therefore well-insulated meristematic layers in which cortical buds are buried (Jacobs), they readily produce shoots from the trunk and branches (Pl. 1 A). Even shrubs which are more easily destroyed, may produce shoots from cortical buds in charred aerial stems, e.g. *Angophora cordifolia, Leptospermum stellatum.*

(*b*) Most remarkable of all is the regeneration from lignotubers which have been described in *Eucalyptus* by Kerr (1925) and Carter (1929). These structures are a peculiar feature of many Australian plants and are most common in the Myrtaceae and Proteaceae (Fig. 5 and Pl. 1 B, C), and are entirely lacking in the Leguminoseae, Rutaceae, Casuarinaceae and most Epacridaceae.

A. Regeneration from subaerial shoots in *Eucalyptus*.



B. Lignotuber of *Lambertia formosa* (Proteaceae) showing the lateral development of subaerial shoots.



C. Development of the lignotuber in seedlings of *Banksia latifolia* var. *minor* (Proteaceae).

An examination of the plants which survive a natural fire shows that the species with lignotubers are rarely killed, while regeneration of plants which do not possess lignotubers is not common (Table 6). The depth below the surface of a lignotuber will be of great importance in its survival. Table 6 gives the location of some of these organs in the soil. From these figures it can be seen that lignotubers are frequently large organs and that they are usually buried sufficiently deeply to avoid high temperatures. Therefore the charring of the top of a lignotuber may occur without causing the death of the plant (Pl. 1 C).

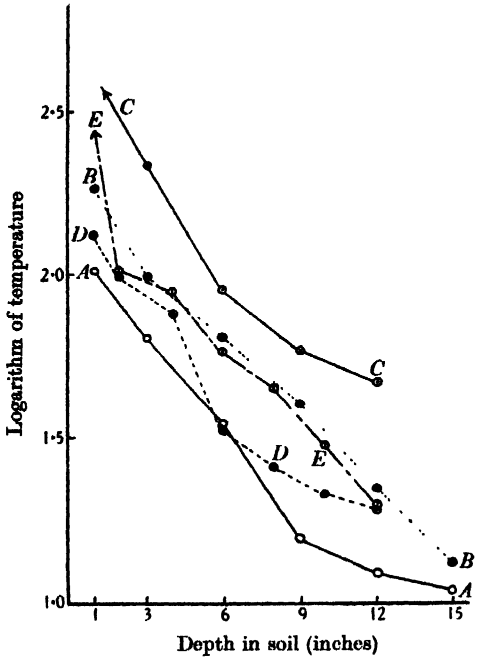


Fig. 4.

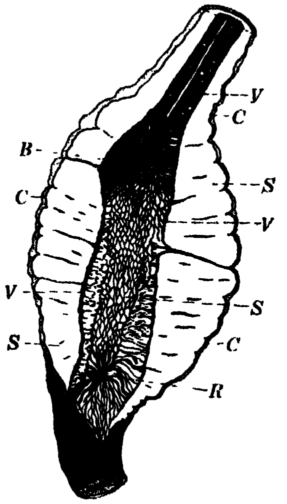


Fig. 5.

Fig. 4. Logarithm of temperature plotted against depth in soil. *A*, from curve *A*, Fig. 1; *B*, curve *B*, Fig. 1; *C*, curve *C*, Fig. 1; *D*, curve *A*, Fig. 3; *E*, curve *B*, Fig. 3.

Fig. 5. Longitudinal section of the lignotuber of *Banksia serrata* (Proteaceae). *V* = vascular tissue; *S* = starch storage tissue; *C* = cork; *R* = section through a large lateral root; *B* = section through a branch. $\frac{1}{4}$ natural size.

B. *Development of seedlings*

Notwithstanding the possibility of destruction or inactivation of seed by fire, the number of seedlings which appears in a burned area far exceeds the number in an unburned area of the same dimensions (Table 7).

These figures show that there is a significant increase in the number of seedlings after fire in all communities, the increase being most conspicuous in moist communities (moist scrub and moss mats). This point is further emphasized by the figures quoted in Table 8, which show that there is a

Table 6. *Location in the soil of some lignotubers and the percentage survivors of species with and without lignotubers*

Name	Lignotuber Presence + Absence −	Depth in soil (in.)		Percentage of plants which survive fire
		Upper surface	Lower surface	
Angophora cordifolia	+	0	9	100
Banksia latifolia var. *minor*	+	0	5	100
B. serrata	+	0	8–9	100
B. spinulosa	+	0	5–6	100
Hakea dactyloides	+	0	5	100
Leptospermum stellatum	+	0	6	100
Lomatia salaifolia	+	4	8	100
Petrophila pulchella	+	2	4	92
Banksia ericifolia	−	.	.	12
Casuarina rigida	−	.	.	0
Hakea gibbosa	−	.	.	0
H. pugioniformis	−	.	.	0
Leptospermum scoparium	−	.	.	0

Table 7. *Number of seedlings before and after fire. Counts done in same general locality, on same day, 5 months after fire*

Community	Number of seedlings per sq. m.			
	Burned		Unburned	
	Mean	σ	Mean	σ
Eucalyptus forest	27	13·4	4	1·7
Moist scrub	342	222·0	7	3·7
Dry scrub	19	8·2	4	2·4
Moss mat	Over 1000	—	32	13·6

Table 8. *Water content of the soil and seedling frequency 5 months after fire. All soil samples were collected, and all counts were done on the same day, no rain having fallen for the last month*

Community	Percentage soil moisture calculated on oven-dried (110° C.) soil	Number of seedlings per sq. m.
Moss mat	47·4	700–800
	51·9	approx. 800
Moist scrub	26·8	240
	31·3	280
Eucalyptus forest	5·1	25
	8·8	51

definite relationship between the water content of the soil and the number of seedlings.

The development of these large numbers of seedlings can be attributed to (*a*) the dehiscence of woody fruits, and (*b*) the ability of the seeds to resist high temperatures.

(*a*) *Dehiscence of woody fruits.*

Many species, particularly members of the Proteaceae, Myrtaceae and Casuarinaceae, possess hard, woody fruits which remain attached to the plant for years after the seed is mature. The retention of the seed on the plant is not an essential process since the fruits on heating over a flame liberate their seeds, which are viable. The advent of a fire causes the simultaneous dehiscence of these fruits, so that the number of viable seeds liberated after fire is very large (Table 9), whereas under natural conditions, since the fruits do not dehisce, the frequency of the seed in the soil is relatively low.

Table 9. *Potential seed production per plant of some plants which produce woody fruits*

Name	Potential seed production per plant: Maximum recorded	Potential seed production per plant: Mean for 10 plants
Banksia ericifolia	2,900	2,300
B. serrata	5,000	2,500
B. latifolia var. *minor*	930	560
Casuarina rigida	83,000	54,000
Hakea gibbosa	150	80
H. pugioniformis	1,200	800
Leptospermum scoparium	106,000	49,000
Petrophila pulchella	13,000	4,600

(*b*) *Resistance of seeds to high temperatures.*

The seeds of all species investigated are relatively resistant to high temperatures when compared with such seeds as those of wheat, sunflower or peas. Table 10 gives the percentage germination, after treatment at various high temperatures in the dry state, of a few common species. These figures show that a temperature of 110° C. for 4 hr. does not greatly reduce the percentage germination, while a few seeds can withstand a temperature of 120° C. or even 130° C. for the same time.

Table 10. *Percentage germination of seeds after subjection to various high temperatures in the dry condition for 4 hr.*

Name	Testa H = Hard S = Soft	Normal percentage germination	Percentage germination after treatment for 4 hr. at (° C.)							
			60	70	80	90	100	110	120	130
Acacia decurrens	H	98	—	—	—	98	72	Nil	—	—
Angophora lanceolata	S	98	—	—	—	—	98	90	16	Nil
Callistemon linearis	S	30	—	—	—	—	30	22	20	4
Casuarina rigida	S	57	—	—	—	—	57	47	Nil	—
Eucalyptus gummifera	S	92	—	—	—	—	92	90	Nil	—
Hakea acicularis	S	100	—	—	—	—	100	88	Nil	—
Leptospermum scoparium	S	25	—	—	—	—	—	25	16	Nil
Peas	S	100	100	84	11	Nil	—	—	—	—
Sunflower	S	100	100	15	Nil	—	—	—	—	—
Wheat	S	100	—	—	100	79	Nil	—	—	—

Since the seed involved in the replacement of the communities is present in the soil before the fire or is liberated from the fruit immediately after the fire, the soil temperature and that within the fruit will be important with reference to the survival of seed during fire. The probable maximal soil temperature at a depth of 1 in. is about 112° C. (Fig. 1, curve *A*), which temperature was reached after the fire had been burning for 2 hr. Therefore seeds which will withstand a temperature of 110° C. for 4 hr. will certainly survive if buried at a depth of 1 in. Also the hard woody fruits, common to many species, act as insulating layers, protecting the seeds during fire.

Not only will the seeds be subjected to high temperatures in the dry state, but also to the action of hot water and steam. Seeds whose testas are permeable to water at any temperature (soft seeds), have a low resistance to high temperatures in the wet condition, comparable with that of peas, sunflower or wheat (Table 11). On the other hand, hard seeds (Rees, 1910, 1911), i.e. those whose testas are impermeable to water at room temperature (18–20° C.), may be subjected to high temperatures in the wet condition for relatively long periods without injury (Table 12). On the contrary, the permeability of the testa is increased so that the percentage of seeds capable of immediate germination is greatly increased.

Table 11. *Percentage germination of seeds after immersion in hot water at various temperatures for* 5 *min.*

	Percentage germination after immersion in water for 5 min. at (° C.)			
Name	50	60	70	80
Peas	100	100	70	Nil
Wheat	100	Nil	—	—
Sunflower	100	100	Nil	—
Hakea acicularis	100	100	100	Nil
Casuarina rigida	57	57	40	Nil
Leptospermum scoparium	25	25	16	Nil
Banksia serrata	100	100	100	Nil

Table 12 gives the results obtained by boiling the seeds of *Acacia decurrens* for various times. The number of seeds which swells during boiling is approximately constant for the different times (Table 12, column 2), showing that the permeability of the testa is independent of the time of boiling. The seeds which swell during boiling are killed, thus behaving similarly to soft seeds. The remainder, after removal from the boiling water, are apparently hard. After 24 hr. the total number of seeds which have imbibed water is 53–70%, while after 6 days 84–97% have swollen. After 10 days the testas of all the seeds are permeable. The percentage germination decreases with the time of boiling (Table 12, column 5 and Fig. 6). Boiling for 5 min. reduces the percentage germination from 98 to 63%, while after boiling for 70 min. the percentage germination is reduced to 3%.

This remarkable resistance to the action of boiling water can be attributed to the ability of the testa to exclude water from the embryo. The testa itself, though apparently impermeable after removal from boiling water, becomes permeable within 10 days, thereby enabling the seeds, which were incapable of germinating under natural conditions, to germinate.

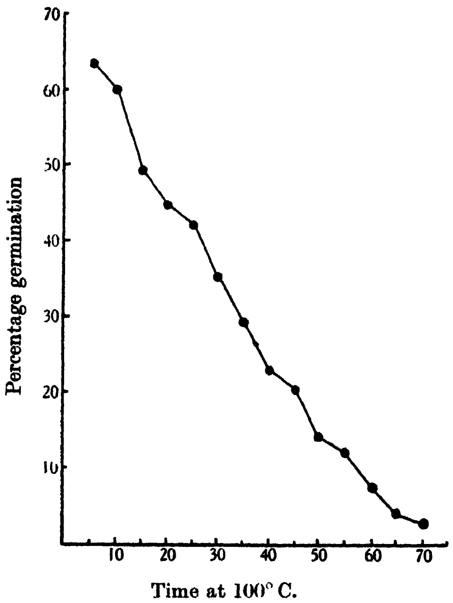


Fig. 6. Percentage germination of hard seeds plotted against time of boiling.

Table 12. *The effect of boiling on the permeability of the testa and percentage germination of the seeds of* Acacia decurrens

Time at 100° C. min.	% of seeds which swell during boiling	% of seeds which swell after 24 hr.	% of seeds which swell after 6 days	Total % germination
5	21	64	92	63
10	15	58	90	60
15	17	62	87	49
20	18	53	84	45
25	15	57	91	43
30	23	62	88	36
35	20	62	91	29
40	13	59	93	23
45	19	54	93	21
50	27	62	96	14
55	23	62	97	12
60	24	61	95	7·5
65	25	70	96	4·5
70	25	65	95	3
Control	—	2	2	98

IV. SUMMARY AND CONCLUSIONS

A method for measuring soil temperatures during forest fires is described and data are given showing the temperatures under various conditions.

During natural fires on the sandstone of the central coastline of New South Wales, the surface temperature varies from 81 to 213° C. At a depth of 1 in. the temperature does not exceed 67° C.

The probable maximal temperature during a severe fire at a depth of 1 in. is 111–114° C.; at 3 in. 59–67° C. Below this level, the soil temperature is not sufficiently high for a long enough period to harm plant organs.

Under extreme conditions (if trees were entirely burned), the temperature at a depth of 1 in. exceeds 250° C., while at a depth of 1 ft. the temperature is 43–50° C.

High percentages of water in the soil greatly retard the conduction of heat. There is not a redistribution of water in the soil after fire; the water is lost to the atmosphere and does not pass downwards and condense.

Fires have no appreciable effect on the physical properties of the soils investigated.

Fires do not kill the vegetation, but many woody plants are capable of regeneration from aerial stems and lignotubers. Plants which possess lignotubers are rarely killed.

After fire, the number of seedlings which appears is very large. This can be attributed to the desiccation and dehiscence of woody fruits and to the ability of the seeds to resist high temperatures.

The seeds of all native plants investigated can resist a temperature of 110° C. for 4 hr. in the dry condition.

The effect of high temperatures on seeds in the wet condition is discussed. Soft seeds are killed after immersion for 5 min. in water at 60–80° C. Hard seeds can withstand the temperature of boiling water for as long as 70 min. when the percentage germination is reduced from 98 to 3 %. Boiling water increases the permeability of the testa, thereby enabling the seed to germinate.

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ON THE ERRORS IN THE ORDINARY USE OF SUBJECTIVE FREQUENCY ESTIMATIONS IN GRASSLAND

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1. INTRODUCTION

THE tests described in this paper were made primarily in connexion with work on chalk grasslands which it is hoped to publish later. The results of these tests have, however, a general bearing on ecological method, and are therefore given separately.

Subjective estimations of frequency, employing symbols such as d. (dominant), a. (abundant), r. (rare), etc., have often been used in ecological studies, especially in Great Britain. On the Continent, subjectively estimated frequency is more often recorded numerically on a 1-5 scale. When such methods are employed, the work is usually in the nature of a descriptive survey requiring no high standard of accuracy. If fine distinctions have to be made, methods of counting individuals, weighing the crop of each species, or calculating percentage cover, are much more satisfactory, provided that a large enough sample can be studied, than any method depending wholly on the judgement of the observer. In many sorts of natural vegetation strictly quantitative sampling methods are very laborious, because the community can only be considered homogeneous over an area so large that the slow and accurate methods take an almost prohibitive length of time.

For certain purposes, therefore, a rapid method of estimation applicable to large areas is very desirable, and the method of subjective frequency estimation is an obvious solution if it is accurate enough for the purpose in view. It has already been shown by Tansley & Adamson (1925), and this paper shows again from another angle, that the errors involved in the method of subjective frequency estimation are very considerable, and it is important to examine how these errors compare in magnitude with the differences which one wishes to study, and what types of plants are most affected.

The tests examined in this paper were all done on the principle of making records twice and comparing the differences. All the examples are from chalk grassland, but similar results might be expected in any herbaceous community composed of many species in close association. Even within the chalk grassland community, however, the amount of error may vary according to the type of grassland, especially according to the length of the grass.

While the errors recorded here are those of a particular person who may be more, or less, accurate and consistent than the average, other observers' records are subject to similar errors. Different observers may, however, attribute different meanings to the symbols used, so that their records are not directly comparable. Although personal differences of this kind may sometimes be important, the question is not examined in this paper.

2. SOURCES OF ERROR

The term "error" is used for lack of an equally convenient word, but strictly the meaning is "difference in subjective frequency symbol due to error or to causes which do not require to be considered in a general survey". Differences arising from sources (2) and (3) below are not errors in the proper sense of the word. Only source (1) is peculiar to the subjective frequency method.

A number of different comparisons may be made between pairs of columns in Table 1, showing the results of different combinations of four sources of error:

(1) Inevitable error.
(2) Annual fluctuation.
(3) Seasonal change.
(4) Individuality of supposedly representative area.

(1) *Inevitable error*

Any series of subjective estimates is liable to what may be called an "inevitable error", shown by the fact that under identical circumstances one does not obtain the same records twice running. The magnitude of this error is suggested by a comparison of cols. 1 and 2 of Table 1. The data are compared quantitatively in subsequent pages. Of course, no reference was made to the first list in compiling the second. In order that the circumstances should be in all material respects the same, the two occasions of listing the area had to be within a few days of each other. Without this precaution there might have been a change in the flowering or fruiting of some species, altering their conspicuousness. The short lapse of time introduces the possibility of a subconscious memory on the second occasion of the symbols already given. There was certainly no conscious memory, but it should be borne in mind that the amount of error revealed may be a slight understatement.

The inevitable error is present *de natura* as an adjunct to all the comparisons dealt with below.

(2) *Annual fluctuation*

The changes in grassland composition between one year and the next, often due to the influence of weather, may be considerable. Such changes have been studied in detail at the Rothamsted Experimental Station (Brenchley, 1935). Cols. 4 and 5 of Table 1 illustrate the differences arising from inevitable error and the effect of a different year. The weather of the two years differed to an average degree. The season was approximately the same, the lists being made on 7 October 1936 and 7 September 1937.

Cols. 13 and 14 of Table 1 provide a similar comparison with an interval of two years.

Differences arising from this and the following source are not significant in a study of changes in the same area over a long period, nor in a general comparison of different areas in the same year or in different years.

(3) *Seasonal change*

The possible importance of change in abundance or aspect of a species with the season of the year needs no emphasis. Although the quantity and quality of seasonal effect varies according to the actual months compared, the sort of discrepancy to be expected is shown by comparing the records in col. 6 of Table 1 (25 May 1937) with those from the same area, given in col. 5 (7 September 1937).

When the whole summer has to be used for field work, and observations may be made as early as May or as late as October, it is important to recognize the difference in recording that may be obtained on the same area.

(4) *Individuality of supposedly representative area*

The differences due to recording two separate areas on the same hillside, plus the inevitable error, are shown by cols. 7 and 8 of Table 1.

A general survey of grassland, such as that made by Tansley & Adamson (1925, 1926), usually involves the study of a small supposedly representative part of a larger area. The question is therefore pertinent: how different is one "representative" part from another? The difference is bound to be more serious the more variable the grassland of the locality, but the general practice is only to study places where an extensive area appears homogeneous. The records from the two Beachy Head areas 37*a* and 37*b* (Table 1, cols. 7, 8) of closely similar facies and listed on the same day, test this point.

Combined effect of the sources of error

Cols. 10 and 11 of Table 1 record the combined effect of the four items dealt with severally in the preceding sections.

The lists were made in different years. The seasonal interval (12 June 26 July) is less than that between cols. 5 and 6, but in the months of June and July the floral aspect changes rapidly, and the less heavily grazed herbage of Tottington Hill reveals seasonal differences which are obscured in the closely cropped turf at Downley Bottom. Area 19, on Tottington Hill, is not defined by any precise limits or landmarks and on a second visit one does not survey exactly the same piece of ground, although a fair proportion of it may be covered again. This is essentially the same type of error as that described under the heading of "individuality of area".

The composite error, arising from all the four causes dealt with above, applies to the majority of records in the chalk grassland studies at present in hand.

3. INTERPRETATION

The following symbols, and combinations of them, have been used in the tests. The status arbitrarily assigned to each relative to the rest is expressed in the arrangement of the list.

d. = dominant
c.d. = codominant
v.a. = very abundant
a. = abundant
f. = frequent
o. = occasional
r. = rare l. = local(ly)

Each symbol is regarded as one unit away from that on the next line, except c.d., which is half a unit away from d. on one side and v.a. on the other. l. used alone has the same status as r. l. as a prefix is taken to lower the status by one unit, e.g. l.a. = f. Absent is regarded as being one place below rare or local.

In comparing pairs of the writer's records in the following analysis of results, standards ("agreement classes") have been used with the meaning given below. Where comparison is made with records of Tansley & Adamson, these standards are adapted as explained later.

Agreement classes. "Exact agreement" implies that identically the same symbol was given on both occasions.

"Approximate agreement" implies that the symbols differ by less than one whole place, e.g. r. and l., f. and f.-a., a. and a., l.c.d.

"Intermediate" implies that the symbols differ by one place, e.g. f. and a., v.a. and d.

"Disagreement" implies that the symbols differ by more than one place, e.g. r. and f., l.c.d. and d.

In certain cases personal judgement has been necessary, e.g. in deciding whether the difference between absent and l.v.a. is "intermediate" or "disagreement". Symbols prefixed by l. have been dealt with somewhat loosely. The verdict in such cases may depend largely on the habit of occurrence of the species, for instance whether it is liable to grow densely where it grows at all, or whether patches showing local dominance or abundance are commonly extensive or not. In several cases of this kind the field notes contain comments which decide the matter.

4. RESULTS

The important points emerging from the primary data in Table 1 are set out in Tables 2 and 3. Besides results from the tests already explained, the tables show certain others under B, F, H, J and L.

B, F and J are figures derived from a comparison of data from the 1920–1 survey by Tansley and Adamson (Tansley & Adamson, 1925, 1926) with the

Table 1. *Primary data. Subjective frequency symbols given in the field by the author*, 1935–8, *and similar data* (*cols*. 3, 9 *and* 12) *obtained by Tansley & Adamson in* 1920 *and* 1921

Col. no. ...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Site ...	Chalton Down, Summit		HB 9. Downley Bottom, area B				37. Beachy Hd.		19. Tottington Hill			HB 18. Butser Hill, S.E. slope			
							Area *a*	Area *b*							
Date ...	26. vii. 38	29. vii. 38	—. ix. 20	7. x. 36	7. ix. 37	25. v. 37	17. viii. 36		1921	26. vii. 35	12. vi. 36	1920	29. ix. 36	26. vii. 38 (1)	(2)
Achillea millefolium	f.	f.	f.	a.	o.	o.-f.	.	.	a.-l.v.a.	l.f.	r.	.	.	.	.
Agrimonia eupatoria	.	.	.	.	.	.	.	.	.	.	r.	.	.	.	.
Agrostis spp.	o.	o.-l.c.d.	a.	a., l.c.d.	a.	f.	.	.	f.	.	r.	.	.	o.	l.
Anacamptis (Orchis) pyramidalis	.	.	.	.	.	.	.	.	r.	.	.	.	.	.	.
Anthoxanthum odoratum	l.	o.	o.	.	.	o.	.	.	v.a.	l.a.	f.	.	.	.	.
Anthyllis vulneraria	.	.	.	.	.	.	o.	.	l.a.	.	.	.	.	.	.
Arenaria serpyllifolia	.	.	.	.	.	.	.	.	.	l.	.	.	.	.	.
Arrhenatherum elatius	.	.	.	.	.	.	.	.	l.	l.d.	.	.	.	.	.
Asperula cynanchica	o.-f.	f.	o.	o.	f.	.	a.	a.	o.	l.	.	a.	a.	a.	a.
Avena pratensis	.	o.	f.-l.a.	r.	r.,	r.	f.	o., l.f.	v.a.-d.	o.	o.	a.	a.	o.	a.
A. pubescens	r.	r.	f.	.	.	.	.	.	a.	a.	o.	f.	.	.	r.
Bellis perennis	o.	f.	.	.	.	.	a.	.	.	.	.	.	o.	f.	f.
Blackstonia perfoliata	.	.	.	.	.	.	r.	r.	.	.	.	.	.	.	.
Brachypodium pinnatum	.	.	.	.	.	.	.	l.d.	o., l.d.	l.	.	.	.	.	.
B. sylvaticum	.	.	.	.	.	.	.	.	.	r.	l.	.	.	.	.
Briza media	a.	o., l.f.	.	a.	a.	r.	f.	a.	a.	f.	f.	o.	a.	a.	a.
Bromus erectus	.	.	.	.	.	.	.	.	l.a.-l.d.	c.d.	f.-l.d.	.	.	.	.
Campanula rotundifolia	o.	a.	o.-f.	a.	a.	a.	.	.	f.	f.	.	f.	a.	o.	a.
Carex caryophyllea	a.	a.	l.a.	o.	f.	a.	o.	l.f.	.	r.	f.	l.a.	f.	a.	a., l.v.a.
C. flacca	a.	a.	v.a.	f.	a.	a.	a.	a.	o.	f.	a.	a.	a.	a.	v.a.
Carlina vulgaris	.	.	.	.	.	.	r.	r.	.	.	.	o.	o., l.f.	r.	r.-o.
Centaurea nemoralis	.	.	.	.	.	.	r.	r.	o.-f.	f.	f.	.	.	.	.
Centaurium umbellatum	.	.	.	.	.	.	l.	.	.	.	.	.	.	.	.
Cerastium vulgatum	o.	r.	o.	.	.	r.	.	.	r.	l.	r.	.	.	.	.
Chrysanthemum leucanthemum	.	.	r.	.	.	.	.	.	.	r.	r.	.	.	.	.
Cirsium acaule	f.	f.-a.	f.	o.-l.f.	f.	a.	f., l.a.	f., l.a.	f.	f.	a.	a.	f.	f.-a.	f.-l.a.
C. arvense	.	.	.	r.	.	.	.	.	.	.	.	.	.	.	.
C. lanceolatum	r.	r.	.	l.	r.	r.	r.	.	.	.	r.	.	.	.	r.
C. palustre	.	.	f.	o.	o.	o.	.	.	.	.	.	.	.	.	.
Clinopodium vulgare	.	.	.	r.	r.	r.	.	.	.	.	.	.	.	.	.
Coeloglossum viride	r.	r.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crepis capillaris	o.	f.	.	o.	o.	.	.	.	.	.	.	.	.	.	.
Cynoglossum officinale	r.	r.	.	.	.	.	.	.	.	r.	r.	.	.	.	.
Cynosurus cristatus	o.	o.	l.	.	.	.	.	.	l.	.	.	.	.	.	.
Dactylis glomerata	.	.	.	.	.	.	f.	.	l.a.	a.-c.d.	a.	.	.	.	.

Table 1 (*continued*)

Col. no. ...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Site ...	Chalton Down, Summit		HB 9. Downley Bottom, area B,				37. Beachy Hd.		19. Tottington Hill			HB 18. Butser Hill, S.E. slope			
							Area *a*	Area *b*							
Date ...	26. vii. 38	29. vii. 38	—. ix. 20	7. x. 36	7. ix. 37	25. v. 37	17. viii. 36		1921	26. vii. 35	12. vi. 36	1920	29. ix. 36	26. vii. 38 (1)	(2)
Daucus carota	.	.	.	.	.	.	r.	r.	.	.	.	.	.	.	.
Deschampsia caespitosa	.	.	.	.	.	.	.	.	l.	.	.	.	.	.	.
Euphorbia exigua	.	.	.	.	.	.	l.	r.	.	.	.	.	.	.	.
Euphrasia brevipila	.	.	o.	.	.	.	.	.	.	.	.	.	.	.	.
E. nemorosa	r.	r.	f.	f.	a.	o.	r.	r.	.	.	.	.	o.	r.	r.
Festuca elatior	.	.	.	.	.	.	.	.	l.	.	.	.	.	.	.
F. ovina	c.d.	v.a.-c.d.	v.a.	f.	c.d.	v.a.-c.d.	d.	c.d.	f.	c.d.	a., l.c.d.	d.	d.	d.	d.
F. rubra	v.a.	v.a.-c.d.	.	v.a., l.c.d.	r.	o.	o.	o.	f.	l.a.	f.	.	a.	a.	a.
Filipendula hexapetala	.	.	.	.	.	.	a.	a.	o.-f.	a.	l.f.	.	.	.	.
Fragaria vesca	.	.	.	.	.	r.	.	.	.	.	.	.	.	.	.
Galium cruciata	.	.	.	r.	.	.	.	.	.	.	.	.	.	.	.
G. erectum	r.	r.	.	.	r.	l.	o.	r.	o.	f.	r.	.	.	r.	r.
G. verum	r.	r.	a.	o.	a.	f.	.	.	f.	l.f.	r.	.	.	.	.
Gentiana axillaris	.	.	o.	.	r.	r.	.	.	.	.	.	.	o.	.	.
Gymnadenia conopsea	.	.	.	.	.	.	.	.	o.	r.	.	.	.	.	.
Helianthemum nummularium	.	.	a., l.d.	l.-d.	o.-l.c.d.	v.a.-l.d.	.	.	.	.	.	.	.	.	.
Hieracium pilosella	f.	a.	l.	r., l.f.	o.-f.	f.	a.	a.	.	.	.	l.	o.	o., l.f.	a.
Hippocrepis comosa	r.	r.	l.	.	.	.	r.	.	l.d.	l.	.	.	.	.	.
Holcus lanatus	.	.	.	l.	l.f.	o.	.	.	o.	.	.	.	.	.	.
Hypochaeris radicata	.	.	.	.	.	.	f.	o.	.	.	.	.	.	o.	r.
Koeleria cristata	f.	a.	r.	a.	a.	a.	a.	a.	f.-a.	a.	r.	.	r.	a.	a.
Leontodon autumnalis	.	.	o.	.	.	o.	r.	.	.	.	.	o.	.	.	.
L. hispidus	l.	.	f.	o.	o.	ó.	r.	o.	o.	a.	f.-l.a.	o.	.	.	r.-o.
L. nudicaulis (Thrincia hirta)	f.	a.	.	.	.	.	a.	a.	.	.	.	.	f.	f.	f.
Linum catharticum	r.	r.	f.	r.	f.	f.	o.	o.	o.-f.	.	o.	a.	f.	.	r.
Listera ovata	.	.	.	.	.	.	.	.	.	.	r.	.	.	.	.
Lolium perenne	.	.	.	r.	.	.	.	.	.	.	.	.	.	.	.
Lotus corniculatus	a.	a.	a., l.d.	a.	a.	a.	f.	f.	f.	l.a.	f.	a.	a.	a.	a.
Luzula campestris	o.	o.-f.	o.	o.	r.	r.	.	.	f.	.	r.	.	.	.	.
Medicago lupulina	r.	r.	.	r.	.	.	o.	r.	.	.	.	.	.	.	r.
Myosotis arvensis	.	.	.	r.	r.	r.	.	.	.	.	.	.	.	.	.
Ononis repens	.	.	.	.	.	.	r.	.	.	.	.	.	.	.	.
Orchis maculata	.	.	.	.	.	.	.	.	.	.	r.	.	.	.	.
Phyteuma tenerum	.	.	.	.	.	.	o.	o.	a.	f.	f.	.	.	.	.
Picris hieracioides	.	.	.	.	.	.	.	.	r.	.	.	.	.	.	.
Pimpinella saxifraga	.	.	.	.	.	.	.	r.	f.	f.	o.	.	.	.	.
Plantago lanceolata	a.	a.	f.-a.	o.	f.	o.	o.	a.	f.	o.	a.	.	f.	o.	f.

Table 1 (*continued*)

Col. no. ...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Site ...	Chalton Down, Summit		HB 9. Downley Bottom, area B				37. Beachy Hd.		19. Tottington Hill			HB 18. Butser Hill, S.E. slope			
							Area *a*	Area *b*							
Date ...	26. vii. 38	29. vii. 38	—. ix. 20	7. x. 36	7. ix. 37	25. v. 37	17. viii. 36		1921	26. vii. 35	12. vi. 36	1920	29. ix. 36	26. vii. 38 (1)	(2)
P. media	.	r.	o.	r.	l.f.	r.	a.	o., l.a.	l.f.	a.	r.	.	.	.	r.
Poa pratensis	.	.	.	.	.	.	.	.	o.	.	.	.	.	.	.
Polygala vulgaris	r.	r.	.	.	.	l.	r.	f.	l.f.	r.	r.	o.	.	r.	r.
Potentilla erecta	.	.	f.	f.	o.	o., l.f.	.	.	.	.	.	.	.	.	.
Poterium sanguisorba	r.	o., l.f.	a., l.d.	f.	f.-a.	f.	a.	a.	v.a.-c.d.	a., l.c.d.	v.a.	.	r.	.	l.
Primula veris	.	l.	l.	.	.	.	.	.	o.-l.a.	l.a.	l.a.	.	.	.	r.
Prunella vulgaris	r.	r.	o.	f.	f.	o.	f.	o.	o.	r.	.	o.	r.	r.	r.-o.
Ranunculus bulbosus	r.	f.	r.	.	.	.	r.	r.	o.	.	o.	o.	r.	r.	r.
Reseda lutea	.	r.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rumex acetosa	r., l.f.	f.	.	.	.	.	.	.	o.	.	.	.	.	.	.
Scabiosa columbaria	f.	f.	o.	.	r.	.	.	o.	o.	r.	.	.	.	.	.
Senecio integrifolius	.	.	.	.	.	.	.	.	o.-f.	r.	o.	.	.	.	.
S. jacobaea	r.	r.	o.	r.	o.	o.	r.	r.	o.	o.	r.	o.	r.	r.	r.
Sieglingia decumbens	.	.	.	.	.	.	r.	.	.	.	.	.	.	.	.
Sonchus asper + oleraceus	.	.	.	r.	.	.	r.	r.	.	.	.	.	.	.	.
Stachys officinalis	.	.	.	.	.	.	r.	.	.	.	.	.	.	.	.
Succisa pratensis	.	.	.	.	.	.	.	.	l.	a.	f.	.	.	.	.
Taraxacum spp.	r.	r.	.	r.	r.	r.	.	.	r.	r.	.	r.	.	r.	o.
Teucrium scorodonia	.	.	.	r.	r.	r.	.	.	.	.	.	.	.	.	r.
Thymus serpyllum	f.	a.	l.a.	f.	a.	a.	a.	a.	o.	l.	.	a.	a.	a.	a.
Tragopogon minus	.	.	.	.	.	.	.	.	r.	r.	.	.	.	.	.
Trifolium pratense	r.	f.	f.	.	r.	.	.	.	f.	r.	.	.	.	.	.
T. procumbens	r.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
T. repens	f.	a.	l.r.	r.	r.	.	.	.	o.	.	.	.	r.	.	.
Trisetum flavescens	f.	f.	.	.	o.	r.	.	.	f.	r.	.	.	.	.	.
Urtica dioica	.	.	.	.	r.	.	.	.	.	.	.	.	.	.	.
Veronica arvensis	.	.	r.	.	.	f.	.	.	.	.	.	.	.	.	.
V. chamaedrys	r.	.	l.	r.	o.	l.f.	.	.	l.	.	r.	.	.	.	.
V. officinalis	.	.	.	r.	.	.	.	.	.	.	.	.	.	.	.
Vicia cracca	.	.	.	.	.	.	.	.	r.	.	.	.	.	.	.
Viola hirta	.	.	l.a.	f., l.a.	f.	a.	o.	o.	o.	o.	r.	f.	o.	o.	o.
V. riviniana	.	.	r	r.	r.	r.	.	.	.	.	.	.	.	.	.

Table 1 (*continued*)

Col. no. ...	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Site ...	Chalton Down, Summit		HB 9. Downley Bottom, area B				37. Beachy Hd.		19. Tottington Hill			HB 18. Butser Hill, S.E. slope			
							Area *a*	Area *b*							
Date ...	26. vii. 38	29. vii. 38	—. ix. 20	7. x. 36	7. ix. 37	25. v. 37	17. viii. 36		1921	26. vii. 35	12. vi. 36	1920	29. ix. 36	26. vii. 38 (1)	(2)
Bryophytes:															
Barbula unguiculata	.	.	.	a.	a.	*	.	.	.	.	.	.	.	.	.
Brachythecium purum	r.	o.	f.	a.	o., l.f.	a.	l.	.	a.	f.	.	a.	r.	r.	r.
B. rutabulum	r.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bryum caespiticium	.	.	.	f.	r.	*	.	.	.	.	.	.	.	.	.
B. inclinatum	.	.	.	.	r.	*	.	.	.	.	.	.	.	.	.
Camptothecium lutescens	r.	o.	l.	.	r.	l.f.	.	l.	.	.	.	a.	r.	.	r.
Ceratodon purpureus	r.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicranum scoparium	r.	r.	l.	r.	r.	o.	.	.	l.	o.	o.	.	o.	r.	r., l.f.
Eurynchium striatum	.	.	.	r.	.	.	.	.	.	.	.	.	.	.	.
Fissidens taxifolius	.	r.	.	r.	o.	.	a.	f.	.	.	.	.	o.	r.	a.
Hylocomium splendens	.	.	.	.	.	.	.	.	f.-l.a.	.	f.	.	.	.	.
H. squarrosum	a.	a.	o.	.	.	.	.	.	f.	r.	r.	.	.	.	r.
H. triquetrum	r.	r.	a.	l.	l.f.	r.	.	.	a.	a.	f.	.	.	.	.
Hypnum chrysophyllum	.	.	.	.	.	.	.	.	.	.	.	.	.	o.	a.
H. cupressiforme	.	.	.	.	r.	.	a.	f.	.	.	.	.	.	.	o.
H. cuspidatum	f.	f.	.	l.	r.	r.	.	.	o.	.	.	.	.	.	.
H. molluscum	.	.	.	.	.	.	.	.	.	.	.	f.	.	r.	r.
Mnium affine	.	.	.	r.	.	.	.	.	.	.	.	.	.	.	.
Neckera crispa	.	.	.	.	.	.	.	.	.	.	.	a.	.	.	r.
Trichostomum tortuosum	.	.	.	.	.	.	.	.	.	.	.	f.	.	.	.
Weisia crispa	.	.	.	.	.	.	a.	.	.	.	.	.	.	l.	r.
W. crispata	.	.	.	.	l.v.a.	*	.	.	.	.	.	.	.	.	.
W. tortilis	.	.	.	.	.	.	.	a.	.	.	.	.	.	.	.
Lichens:															
Cladonia fimbriata	.	.	.	.	.	.	.	.	.	.	.	f.	r.	.	r.
C. rangiformis	.	.	.	.	.	.	l.a.	o., l.a.	.	.	.	.	l.f.	o.	f.
Collema pulposum	.	.	.	.	.	.	.	.	.	.	.	.	.	r.	r.
Collemaceous sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r.
Peltigera canina	.	.	.	.	.	.	.	.	.	.	.	o.	.	.	.
Total number	54	54	50	54	56	54*	50	43	65	52	47	29	32	34	50

* Acrocarpous mosses not noted on this occasion. The total of 54 includes the acrocarpous mosses of the previous column.

writer's data of 1935 and 1936 from the same areas. A difficulty involved in considering these results is that the two sets of observations were made by different workers, who attach a different meaning to some of the symbols. This question has been examined and any details necessary will be given in a later paper with the results to which they apply. The figures for cols. B, F and J in Table 3 have been derived after making allowance for the different standards of the different workers, and may be regarded as fairly satisfactory.

Under H are given figures derived from a comparison of two grassland areas distant from one another. They are on casual inspection obviously different, but not unusually so. They represent types which, in ecological work, one might well wish to compare, and it is essential to know how the agreement classes derived from comparing two such areas stand in relation to those resulting purely from error.

The figures under L give a comparison between the results of a more thorough and a less thorough search of the same area, a matter dealt with on pp. 205–7.

Specific content of lists

The main information in Table 2 is given by the figures showing the number of species common to both occasions (e.g. first and second time of listing) expressed as a percentage of the total number found on the two occasions. The results mainly follow expectation. The largest number of species (83 %) is held in common between the two lists testing inevitable error alone. There are somewhat lower numbers in common in the tests of the other sources of error individually. These errors acting together give a yet lower number. Then come the comparisons which involve a lapse of 16 years (J, 49 %; B, 46 %); these are well below the lowest value due to errors only (G, 60 %) so that there has probably been a floristic change. Finally comes H, the comparison of two distant grassland areas differing to an average extent. They have only 25 % of their species in common, so that there is obviously a very real floristic difference. The one unexpected result is under F, where lists of area 19 made in 1921 and 1935, subject to all errors, actually have more species in common than appear under G, which represents the same area and same errors without the 14-year interval. The inference must be that no significant floristic change has taken place in this interval notwithstanding any change which may have occurred in the frequency of individual species.

Purely floristic comparisons of course reveal less, of errors and of real differences, than comparisons of frequency. The latter are dealt with next.

Frequency of species

Comparison of the frequency symbols in Table 1 is given in Table 3 in the form of agreement classes. Cols. H and L need not be considered for the present.

As between the tests of error (A, C, D, E, G, K), and the comparisons of

Table 2. *Comparison of the numbers of species in certain pairs of columns of Table 1. The lists under comparison are indicated by the first line in this table; thus "1 and 2", "3 and 4", etc. The percentage numbers are percentages of the figure given in the top row (grand total)*

Causes of difference in records

A. Inevitable error.
B. Inevitable error. Annual fluctuation. 16 years interval.
C. Inevitable error. Annual fluctuation.
D. Inevitable error. Seasonal change.
E. Inevitable error. Individuality of "representative" area.
F. Inevitable error. Annual fluctuation. Seasonal change. Individuality of area. 14 years interval.
G. Inevitable error. Annual fluctuation. Seasonal change. Individuality of area.
H. Two distinct localities. Errors as under G.
J. Inevitable error. Annual fluctuation. Seasonal change. 16 years interval.
K. Inevitable error. Biennial fluctuation.
L. Comparison of ordinary and specially careful recording

	A	B	C	D	E	F	G	H	J	K	L
Columns of Table 1 compared	1 and 2	3 and 4	4 and 5	6 and 5	7 and 8	9 and 10	10 and 11	11 and 13	12 and 13	13 and 14	14 and 15
Grand total of species found on both occasions	59	71	64	62	55	70	62	63	41	40	50
Percentage found on first occasion	91	70	84	87	91	93	84	75	71	80	68
Percentage found on second occasion	91	76	87	90	78	74	76	51	78	85	100
Percentage common to both occasions	83	46	72	77	69	67	60	25	49	65	68
Percentage found on first occasion only	8	24	12	10	22	26	24	50	22	15	0
Percentage found on second occasion only	8	30	15	13	9	7	16	25	29	20	32

Table 3. *Comparison by agreement classes (defined on p. 196) of frequency symbols in certain pairs of columns of Table 1. The lists under comparison are indicated by the first line in this table ("1 and 2", "3 and 4", etc.). The figures are percentages of the grand total of species for the two lists*

Causes of difference in records. As in Table 2

	A	B	C	D	E	F	G	H	J	K	L
Columns of Table 1 compared	1 and 2	3 and 4	4 and 5	6 and 5	7 and 8	9 and 10	10 and 11	11 and 13	12 and 13	13 and 14	14 and 15
Exact agreement	44	6	27	32	40	10	16	8	15	32	36
Approximate agreement	8	20	12	16	9	21	14	0	12	8	12
Intermediate	36	50	49	36	33	42	47	48	32	40	38
Disagreement	12	24	12	16	18	27	23	44	41	20	14

records of Tansley and Adamson with those made by the writer after 14–16 years' interval (B, F, J), the range of approximate agreement and intermediate values scarcely differs significantly. The most significant case is that of the disagreement class, which ranges from 12 to 23% in the tests of error; and from 24 to 41% when the 15 years' interval is involved, making a real change likely. These figures include allowance for the difference of symbol due to the records being made by different workers. The obvious difference in the range of exact agreement values (tests of error, 16–44%: involving 15 years' interval, 6–15%) is largely a reflexion of the differences in the disagreement class.

The lowest disagreement value of all is shown by the test of inevitable error alone (A, 12%). The highest disagreement value among the tests of error is produced by the four sources combined (G, 23%). These results both follow expectation. On the area of the latter test (G), a 14-year interval has produced a disagreement class only slightly larger (F, 27%) suggesting that the change in 14 years has been slight unless among the disagreeing species are any of quite unmistakably altered frequency and notable ecological significance (cf. p. 201, floristic similarity). The largest disagreement shown in Table 3 is that resulting from the comparison of two distinct localities (H), again what would be expected. With a value of 44% disagreement, it is so far removed from the greatest due to error (23%) that a significant difference in vegetation is clearly indicated.

Characteristics of species liable to the different sources of error

For the interpretation of results obtained by the subjective frequency methods, it is of more practical importance to see which species are least, and which most, liable to disagreement in recording in the case of inevitable error alone; which in the case of annual fluctuation, of seasonal effect, of individuality of representative area. And in each case, is there a common characteristic of the group of species? If so, it will be possible to make suitable safeguards in interpreting records, according to the characteristics of the species under consideration and the conditions under which the compared records were made.

Inevitable error alone (Table 1, cols. 1 and 2). Seven species show disagreement. The symbols by which they were recorded in the two lists are given:

Avena pratensis	abs.	o.
Briza media	a.	o.l.f.
Campanula rotundifolia	o.	a.
Poterium sanguisorba	r.	o.l.f.
Ranunculus bulbosus	r.	f.
Rumex acetosa	r.l.f.	f.
Trifolium pratense	r.	f.

The first two species are grasses, difficult to assess in grazed turf owing to the small units in which they occur and the narrowness of the leaves. *Campanula rotundifolia* and *Ranunculus bulbosus* exist as plants of varying size, some being extremely small. There is no obvious cause for the error in the remaining three species; it is probably a matter of chance.

Annual fluctuation (Table 1, cols. 4 and 5, 13 and 14). This factor was tested on two different areas, the interval in one case actually being two years.

The following species show disagreement (the only one doing so in both tests being *Linum catharticum*):

Achillea millefolium

(1)
Agrostis spp.
Avena pratensis
Campanula rotundifolia
Festuca ovina
F. rubra
Galium verum
Koeleria cristata
Trisetum flavescens

(2)
Brachythecium purum
Bryum caespiticium
Hypnum chrysophyllum

(3)
Carlina vulgaris
Gentiana axillaris
Linum catharticum

The three sets of species printed in groups form fairly clear categories, the first being grasses and other narrow leaved plants, the second bryophytes, and the third annuals or biennials. Groups (1) and (2) and *Achillea millefolium* probably owe their disagreement mainly to the inevitable error of the method, and group (3) to fluctuation in abundance. There is a preponderance of grasses in group (1). In the absence of inflorescences, it is particularly hard to distinguish adequately between the two fescues, and between *Trisetum* and the *Agrostis* forms. *Koeleria cristata* is easily confused with *Agrostis* in damp weather and with *Festuca rubra* when rolled up in drought. *Campanula rotundifolia* (see also p. 203) and *Galium verum* have narrow leaves, probably a feature contributing to inconsistent observation.

The difficulty of correctly estimating the frequency of bryophytes is always apparent in the field.

Linum catharticum is on account of its slender dimensions very liable to error (cf. Tansley & Adamson, 1925, p. 187). In addition it is an annual and has been noticed elsewhere to be liable to wide fluctuations from year to year. *Gentiana axillaris* and *Carlina vulgaris*, which are biennials, probably fluctuate likewise to a large extent. Striking examples of such fluctuation in abundance are sometimes shown by *Senecio jacobaea*, a biennial or "induced perennial" (Cameron, 1935). In August 1938, for instance, a certain grazed chalk hillside bore all over it a conspicuous stand of whitened dead stalks of ragwort which must have grown in 1937 or perhaps 1936; but almost no living plants were visible.

In view of such possibilities it is inadvisable to assume that large differences in the symbols of annual or biennial species in lists of different years necessarily indicate a *trend* in the vegetation.

Seasonal effect (Table 1, cols. 6 and 5). Nine species show disagreement. Those marked as more abundant on 25 May 1937 are:

Anthoxanthum odoratum
Asperula cynanchica
Leontodon autumnalis

Veronica arvensis

Brachythecium purum

Among these, *Anthoxanthum odoratum, Asperula cynanchica* and *Veronica arvensis* are known from general observations to be more conspicuous in early summer, when they flower. *Leontodon autumnalis* would be expected to show more in September than in May. The error is probably due to confusion with *Crepis capillaris.*

Species marked as more abundant on 7 September 1937 are:

Briza media
Crepis capillaris
Euphrasia nemorosa
Fissidens taxifolius

Crepis capillaris and *Euphrasia nemorosa* are both known to be more conspicuous in the latter part of the summer.

Five out of the nine species showing disagreement in this test could thus be accounted for by their flowering period rendering them more conspicuous, and one must clearly beware of such species in the comparison of lists made at different seasons. The particular area HB 9 is heavily grazed by rabbits. In one less grazed, flowering would exert a greater influence in the seasonal aspect and presumably cause a greater discrepancy in the frequencies assigned.

Individuality of area (Table 1, cols. 7 and 8). The field notes made when the areas 37*a* and 37*b* were listed state that 37*b* bore the same facies as 37*a*, except that *Leontodon nudicaulis* (*Thrincia hirta*) was less conspicuous and *Poterium sanguisorba* more so. But their recorded frequencies for the two areas show exact agreement, both being abundant.

The species showing disagreement are:

Anthyllis vulneraria
Bellis perennis
Brachypodium pinnatum
Dactylis glomerata
Plantago lanceolata
P. media
Polygala vulgaris
Scabiosa columbaria

Weisia crispa
W. tortilis

The disagreement in some of these is presumably due to inevitable error. The turf was short and the field notes state that the only species conspicuously in flower was *Leontodon nudicaulis.* Under these circumstances none of these ten species in the amounts in which they occurred would contribute notably to the facies, with the possible exception of *Dactylis glomerata* and *Plantago lanceolata. Brachypodium pinnatum* would only do so if its symbol l.d. signified dominance over a considerable area.

Thus a supposedly representative area may not give a typical representation of species whose frequency within normal limits does not greatly affect the appearance of the turf. The ecologist, in choosing a representative area for survey, will of necessity be blind to the irregular occurrence of such species. Fortunately their number is bound to be small, or the facies would be different to the eye.

Care in listing species and assigning frequencies

The foregoing considerations are all involved under ordinary practice. As a supplementary enquiry, records were obtained on an area first in the ordinary manner and afterwards specially carefully. The ordinary survey as practised by the writer has covered an area of about 0·25 hectare (½ acre). The listing of the species is stopped when continued searching for about 5 min. more reveals no previously unrecorded species. The listing and the addition of frequency symbols occupies about ¾–1 hr. To complete the list in this time necessitates writing down the species as met, and putting in frequency symbols afterwards from the impression formed on the mind of the frequency of each species. In the case of some five or six species it is usual that no clear impression comes to mind, or, in the case of inconspicuous plants, that one has small confidence in one's estimate. For these few the area is traversed again, and their frequencies are then inserted.

The results obtained for the test of inevitable error at Chalton Down indicate the considerable inaccuracy of assigning of frequency symbols by this method.

Col. 14 of Table 1 shows the result of surveying area HB 18 in the ordinary manner, and col. 15 the result obtained by making the list of species as usual and then going over the ground again and again, with only one (or occasionally two or three) species in mind each time, estimating the frequency of each in turn. New species noticed while doing this were added to the list. Following this procedure one probably came near to finding every species on the area. With the usual time available and the rich flora involved this is not as a rule attempted on a 0·25 hectare area. This high standard probably gives quite a fair idea of the real composition of the grassland, but the time taken in all was 2¼ hr., a pace usually considered too slow for routine work, and hardly economical since one of the more objective methods could be used if so much time is to be spared.

The differences in the lists are analysed in Tables 2 and 3. Table 2 shows that the number of previously unseen species found while carefully estimating frequencies was 32 % of the total, i.e. the focussing of attention on the turf for about an extra 1¾ hr. made the list about half as long again as the normal. The sixteen additional species found, their frequencies, and, where possible, the probable reason for their omission from the first list are given below:

Avena pubescens	r.	Inconspicuous
Cirsium lanceolatum	r.	Spasmodic
Hypochaeris radicata	r.	Spasmodic
Leontodon hispidus	r.-o.	Confused with L. nudicaulis
Linum catharticum	r.	Inconspicuous
Medicago lupulina	r.	—
Plantago media	r.	Spasmodic
Poterium sanguisorba	l.	Spasmodic
Primula veris	r.	Spasmodic
Teucrium scorodonia	r.	Margin of area
Camptothecium lutescens	r.	Inconspicuous
Hylocomium squarrosum	r.	Inconspicuous
Hypnum cupressiforme	o.	Inconspicuous
Neckera crispa	r.	—
Cladonia fimbriata	r.	—
Collemaceous lichen	r.	Inconspicuous

As regards the frequency symbols given to the thirty-four species appearing in both lists, the position was as follows:

Exact agreement	18	Intermediate	5
Approximate agreement	6	Disagreement	5

The five species common to both lists and showing disagreement of symbols are *Avena pratensis*, *Campanula rotundifolia*, *Hieracium pilosella*, *Fissidens taxifolius* and *Hypnum chrysophyllum*. With the exception of *Hieracium* they are species which from the previously described tests would be regarded as liable to error. These five, and four out of the five showing intermediate agreement, were given their higher frequency symbol in the careful estimation.

5. CONCLUSIONS

The tests above described reveal errors which in certain cases are of startling magnitude. These may reflect to some degree upon the accuracy of the author, but they were deliberately done under conditions where a large error could be predicted, though how large was unknown. The aim is not to see how accurate the method can be under optimum conditions, but how inaccurate it may be under the conditions of customary use, where time available in the field is a potent factor.

A high degree of accuracy is not, of course, always necessary. In studies of long-period changes, or of different grassland types, differences which may be due to the normal year-to-year fluctuations, to seasonal changes, or to local heterogeneity, are only misleading. A method of recording so accurate as to take cognisance of such differences may be unprofitable unless examining these very points. It has, however, been indicated that a large proportion of discrepancy is due to "inevitable error," so that there is clearly room for improved methods which will eliminate this source of inaccuracy.

In view of the many errors in the method, differences which are regarded as real after making full allowance for errors can only be stated in quantitative terms to the extent of saying that a species was more abundant on one occasion than on another; in most cases it is impossible to say how much more abundant.

It is suggested that, if the subjective frequency method has to be used for any work other than very rough description, tests should always be made beforehand and should be repeated from time to time. Such tests are necessary both in planning the procedure to adopt in the field and in the interpretation of results. They would only apply to the particular investigator and type of vegetation.

6. SUMMARY

Tests are described which show the serious errors involved in subjectively assigning symbols such as d., dominant, a., abundant, r., rare, etc. in surveys of grassland vegetation. They were primarily undertaken in connexion with research on chalk grassland, and are necessary to the interpretation of certain results already obtained. The tests consisted in making independent lists for the same area under various conditions and comparing the presence of the species and the frequency given in the two lists. The estimates made in successive trials were often very different.

The main causes of difference are four: the inevitable error of the method, annual or biennial fluctuation in frequency of species, seasonal changes in abundance or aspect, and the individual differences of areas which are parts of a larger supposedly homogeneous area. Only the first of these causes of difference is inseparable from the method; the others are incidental. Frequency estimations of the same species in two lists compared have been described as showing "disagreement" if they are more than one unit different, e.g. r. and f. (see p. 196).

When the only sources of discrepancy were inevitable error and annual or biennial fluctuation, the species showing disagreement amounted in one test to 12% and in another to 20% of the grand total of species in the two lists compared. Where all the four sources of discrepancy were involved (i.e. the same area but with not exactly the same limits, recorded by the same observer on 26 July and 12 June in two successive years), the corresponding figure was 23%. The disagreement between the first of these records and that of the same general area made by different observers 14 years earlier, is only 27%. This figure allows for the differences of meaning (not examined in this paper) attached to the symbols by the different observers.

An examination was made of the species showing disagreement in tests under various circumstances. It indicates that the types of species specially liable to differences arising from the four sources of discrepancy are as follows:

Inevitable error: Grasses, other narrow-leaved plants and bryophytes (all difficult to observe).

Annual (or biennial) fluctuation in abundance: Annuals, biennials.

Seasonal change in abundance or aspect: As would be expected, species showing a marked periodicity through the summer in this respect.

Individuality of supposedly representative area: Species whose frequency within normal limits does not affect the general appearance of the herbage. The number of these in any one area is bound to be small.

A test was made of the effect of listing an area and assigning the frequencies far more carefully than has generally been considered practicable, taking in all about 2¼ hr. instead of an hour. During the additional time spent evaluating frequencies, the number of species in the list was increased by about half of the original number.

The method of assigning frequency symbols subjectively, which may be the only method practicable for certain types of work, is clearly subject to very great errors whose magnitude should be tested under the particular circumstances.

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STUDIES IN THE ECOLOGY OF RIVERS

IV. OBSERVATIONS ON THE GROWTH AND DISTRIBUTION OF THE SESSILE ALGAE IN THE RIVER HULL, YORKSHIRE

By R. W. BUTCHER

(With two Figures in the Text)

INTRODUCTION

THE algae which inhabit natural waters may be conveniently studied as two separate groups. The first group consists of those which are suspended in the water and usually termed plankton: the second group of those which are growing on the bottom or on any submerged objects such as stones, rocks, living plants or dead bodies. This second group has been variously called benthos, the littoral algae or the sessile algae.

Plankton has been extensively studied; in the sea where it is all-important, and in lakes, reservoirs and small ponds. Little attention however has been paid to it in moving waters and quantitative data is very sparse.

Still less information is available about the growth and distribution of the bottom-living and shore living algae. Geitler (1927) and Fritsch (1929) studied the algae on the bed of the small streams in Austria and Devon respectively but in neither case were quantitative data presented.

In 1932 the view was put forward (Butcher, 1932*b*) that as far as plankton and benthos in small shallow rivers were concerned, the plankton represented a pale image of the benthos from which it was almost entirely derived. Additional results in the river Tees (1937) and the Thames (Rice, 1938) support this view though, on the other hand, Southern & Gardiner (1938) have shown that the plankton of the Shannon approaches to a certain extent the plankton of the lakes in the same watershed but even in the figures these authors give, some organisms clearly derived from bottom growths are present. This type of limnetic plankton in moving waters is apparently rare. In most cases water comes out of a lake as a stream in which the flow is obvious and the limnetic organisms are immediately destroyed. In some cases they are filtered out by the tufts of river-plants (1937) and in other instances they are probably pounded to death and their place is taken by algae derived from the river bed (Butcher *et al.* 1937). Conversely it has been found (Metropolitan Water Board, 1938) that the plankton of a large reservoir consists of species totally different from and unrelated to those in the supply water derived from the river Thames.

With all this evidence of the secondary role played by the plankton and the importance of the bottom-living or sessile algae in the rivers of the type usually found in Britain, it is natural that where studies of the flora and fauna have been carried out, work has been concentrated on the sessile algae and the plankton has been ignored.

METHOD OF COLLECTING

For such studies to be of value it was necessary that reliable quantitative data should be obtained and to this end a method was devised which has been described in several papers (Butcher, 1932*a*, *b*; Pentelow *et al.* 1938). Glass slides are fixed in a metal photographic printing frame and left submerged for 20–30 days, usually flat in the river bed, but occasionally, where the water has been deep, hung vertically to a submerged pile. The algae which grow on these slides are subsequently counted direct under the microscope or, if the deposit is very thick, a suspension of an area of growth of about 200 sq. mm. is made up in a litre of water, well shaken to break apart the various algae, and 0·1 ml. of the suspension withdrawn, spread on a ruled slide and the algae counted.

This method gives only roughly quantitative results and it is unlikely that all the algae in a given stretch of water are included. It must also be emphasized that in any case only a minute proportion of the whole area can be examined and the algal growths are not always homogeneous even over very small areas where external factors are apparently constant.

It is hoped that by using such methods the influence on the growth and distribution of algae of the many external factors will be elucidated, though very extensive data will have to be obtained before this hope is realized. Not only is the interplay of the numerous external factors extremely varied but a large number of algae is involved in each case. The difficulties are increased because many of the algae that were found in the course of these studies are undescribed. In addition, reproductive organs and characters of taxonomic value are frequently absent so the descriptions cannot be completed.

Though as yet it appears that we are a long way from our objective of presenting a list of algal communities or separate species which, when present, indicate certain conditions to be found in the water, a considerable mass of data has been collected and it is felt that these are of sufficient value to record in a series of short papers. Some of the rare and little known algae which have been found commonly in the course of these investigations were described by the author (Butcher, 1932*c*).

ALGAE OF THE RIVER HULL

Details of collections from the Lark (Butcher *et al.* 1931), Tees (Butcher *et al.* 1937) and Bristol Avon (Pentelow *et. al.* 1938) have already been published.

The algae now dealt with are those collected in the upper portion of the river Hull, Yorkshire. This stretch is in reality a canal with its terminal point at Driffield where, at the canal head, it is fed by a small stream from the chalk.

There are locks at Driffield ¼ mile below canal head, at Whinhill 1½ miles below Driffield, at Wansford ¾ mile below Whinhill and at Snakeholme ½ mile below Wansford. The canal can thus be described as a series of four lagoons each with a very small flow. A series of observations in October 1931 gave the speeds of flow as 1·0, 1·6 and 4·5 ft. per sec. near Driffield, Whinhill and Snakeholme locks respectively. Adjacent and parallel with the canal and taking the surplus water is a small free-flowing stream known as the West Beck or Driffield Beck the fauna of which has been investigated by Whitehead (1935). The canal and stream unite some distance below Snakeholme and the navigable waterway so formed is then called the river Hull. In these studies the term river Hull should be taken as including both West Beck and Driffield Canal.

CHEMICAL FEATURES

The water supplying the canal at Driffield contains about 18 parts $CaCO_3$/100,000 and it is polluted intermittently by effluents from the local gas-works. Such effluents usually contain among other things tar acids, tar bases, cyanides and high concentrations of ammonia. Except for the last mentioned, these substances are known to be very toxic to fish but their action on algae has not been ascertained.

Below Driffield Lock the effluent from the local sewage works enters the river. This is a fairly constant source of pollution and it produces changes in the water normal to this type of effluent; first it increases the organic matter and ammoniacal nitrogen and depresses the dissolved oxygen; then, as it moves downstream, the organic matter decomposes, nitrites and thereafter nitrates are formed in some quantity and the oxygen content gradually rises. Since the Driffield Canal is very sluggish the decomposition of the organic matter is apparently complete by the time the water reaches Snakeholme.

Frequent estimations were made of ammoniacal nitrogen, nitrate, *p*H and dissolved oxygen between 1930 and 1933 and in a few samples the hardness and total dissolved salts were estimated. For the results I am indebted to the Government Chemist's Department and to Mr Akers.

Table 1. *Mean values of various constituents of Driffield Canal water in 1932; expressed as parts*/100,000

Position	*p*H	Ammoniacal nitrogen	Nitric nitrogen	Organic nitrogen	Oxygen abs. 5 days	Oxygen abs. 4 hrs.	Hardness	
							Perm.	Total
Canal Head	7·5	0·019	0·39	0·059	0·33	0·057	16·5	30·3
Whinhill	7·3	0·087	0·43	0·191	0·46	0·112	18·0	28·8
Wansford	7·5	0·056	0·37	0·076	0·28	0·090	17·6	31·0
Snakeholme	7·5	0·037	0·33	0·084	0·25	0·105	18·7	29·3
West Beck	7·8	Nil	0·40	—	—	—	17·8	—

From the above figures it may be seen that the water is hard and contains a plentiful supply of nitrogenous compounds. Organic matter is highest at Whinhill just below the sewage pollution, while at all the other stations it exceeds the amount found in unpolluted rivers such as the Itchen. The total amount of dissolved salts is also high.

POSITION OF ALGAL COLLECTIONS

The frames of glass slides on which the algae grew were suspended, at an average of 18 in. under water, vertically from the wall of the lock immediately above the upper lock gate at the following places:

Driffield above the sewage effluent.
Whinhill 1½ miles below the sewage effluent.
Snakeholme 2¾ miles below the sewage effluent.

For a short period slides were also laid on the bed of the West Beck in the neighbourhood of Snakeholme.

Collections were made as far as possible at intervals of 28 days. The data are presented in Tables 2–5 and in Fig. 1, but only the commonest algae are considered in detail. A list of the remainder is drawn up as an appendix.

Amount of growth. The numbers of algae that grow on the slides fall into two groups: a winter period from October to March when the numbers are generally low, and a summer period from March to October when the numbers are considerably higher. Except for this differentiation of summer and winter, and a series of low numbers at Driffield in the summer of 1932, no other regular periodicity can be demonstrated.

Though at each station there is a maximum some time in May or in the early summer, this is at no definite date and it cannot, with the data here presented, be related to any other physical or chemical factor. If it had been possible to deal with a greater number of collections the resulting average curve would doubtless have shown a smoother outline.

These figures are rather lower than those recorded for other calcareous waters given in Table 7 and this may be due partly to the vertical position of the slides. After the sewage effluent has entered the river there is a slight decrease (at Whinhill) followed by a very considerable increase at Snakeholme where presumably the organic matter has been completely oxidized. This same increase after organic pollution has been observed both on the Tees and the Bristol Avon.

Species of algae present. When the results are considered from the point of view of the various species which make up the growths it will be found that the dominant algae can be arranged in the following order of frequency:

Cocconeis placentula
Ulvella frequens
Achnanthes minutissima
Gomphonema longiceps
Sphaerobotrys fluviatilis
Stigeoclonium farctum

Other species that were at times common were:

Heterolagynion oedogonii
Chaetopeltis orbicularis
Gomphonema acuminatum
G. constrictum
Characium sieboldi
Stigeoclonium nanum
Achnanthes lanceolata

The remaining species found are given in the algal list in the appendix.

Table 2. *Dominant algae at Driffield Lock in no./sq. mm.*

	1931					1932										1933						
Date of collection ...	30. vii	8. ix	10. x	15. xi	13. xii	24. i	6. iii	8. v	5. vi	23.vi	30.vii	29.viii	27.ix	22. x	26 xi	7. i	4. ii	11. iii	8. iv	6. v	22. vi	22. vii
Ref. no. ...	D 2	D 3	D 4	D 5	D 6	D 7	D 8	D 9	D 10	D 11	D 12	D 13	D 14	D 15	D 16	D 17	D 18	D 19	D 20	D 21	D 22	D 23
Cocconeis placentula	34	400	200	45	250	32	3900	1800	600	200	3	12	3	1	+	6	2	200	200	100	800	3900
Achnanthes minutissima	+	800	+	1	+	+	–	700	1100	1300	1	+	+	+	+	6	6	+	400	500	2800	100
A. lanceolata	–	100	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cymbella spp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Gomphonema spp.	4	200	+	7	+	+	100	1300	500	200	3	1	+	–	+	11	4	100	800	400	500	100
Nitzschia spp.	+	+	–	+	–	–	–	100	100	100	–	+	–	–	–	4	1	+	+	100	+	–
Other diatoms	–	100	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Characium sieboldi	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	100	+	+	–
Sphaerobotrys fluviatilis	2	100	100	7	6	–	100	100	100	100	–	–	+	–	–	18	24	200	400	100	100	+
Chaetopeltis orbicularis	–	+	+	2	–	–	+	100	100	+	+	+	–	–	+	–	–	+	200	100	+	+
Stigeoclonium spp.	+	+	+	2	1	–	+	200	100	+	–	–	–	–	–	3	3	200	100	500	100	100
Ulvella frequens	17	500	200	21	19	2	600	1200	1000	1000	14	3	+	+	+	22	59	600	1100	1500	900	300
Other Chlorophyceae	–	–	–	–	–	–	100	200	100	–	–	–	–	–	–	–	–	–	–	–	–	–
Chamaesiphon spp.	13	–	–	–	–	–	300	–	200	+	–	–	–	–	–	–	–	–	+	+	+	–
Other Myxophyceae	–	–	–	–	–	–	100	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Heterolagynion oedogonii	12	+	+	12	16	15	–	–	–	–	6	8	3	1	2	1	2	–	–	–	–	+
Totals	82	2300	500	96	300	40	5100	5800	4000	3200	29	28	8	3	3	80	104	1600	3300	3400	5500	4700

Table 3. *Dominant algae at Whinhill Lock in no./sq. mm.*

	1931					1932										1933						
Date of collection ...	4. vi	30. vii	10. x	15. xi	13. xii	24. i	6. iii	8. v	5. vi	23.vi	30.vii	29.viii	27.ix	22. x	26. xi	7. i	4. ii	11. iii	8. iv	6. v	22. vi	23.vii
Ref. no. ...	W 1	W 2	W 3	W 4	W 5	W 6	W 7	W 9	W 10	W 11	W 12	W 13	W 14	W 15	W 16	W 17	W 18	W 19	W 20	W 21	W 22	W 23
Cocconeis placentula	127	1900	100	300	104	34	1000	700	1800	400	500	100	300	100	+	3	7	+	500	1100	3000	1600
Achnanthes minutissima	–	–	300	+	8	5	400	300	+	+	400	+	400	200	1	1	7	+	100	500	100	+
A. lanceolata	1	–	+	–	7	2	+	100	+	+	100	–	100	200	+	20	15	200	+	200	+	–
Gomphonema spp.	1	+	100	+	22	4	800	500	+	+	+	+	200	100	+	16	85	+	300	400	100	+
Nitzschia spp.	3	–	+	+	22	5	–	100	100	+	+	+	+	100	–	2	8	+	+	+	100	+
Other diatoms	3	–	+	+	36	2	–	100	+	+	+	–	+	100	+	1	7	+	+	+	+	+
Sphaerobotrys fluviatilis	1	100	100	+	10	–	200	200	+	+	100	+	100	400	–	20	11	200	100	100	100	–
Chaetopeltis orbicularis	3	100	+	100	4	1	100	100	300	200	100	+	100	200	–	9	1	+	200	400	100	+
Stigeoclonium spp.	–	200	+	+	–	1	+	300	300	+	100	+	+	100	–	1	2	+	300	100	+	+
Ulvella frequens	16	900	1000	700	47	13	900	900	300	400	500	300	1000	500	–	35	31	200	1200	500	100	200
Other Chlorophyceae	–	100	+	+	4	–	100	200	200	100	+	+	100	100	–	–	1	–	400	100	300	+
Chamaesiphon spp.	2	–	+	+	–	–	–	–	–	–	–	+	–	–	–	5	–	–	–	–	–	–
Other Myxophyceae	–	–	+	+	–	–	–	–	–	–	–	–	–	100	9	–	–	–	–	–	–	–
Heterolagynion oedogonii	2	+	–	–	60	11	+	–	+	+	+	+	–	+	–	34	–	+	–	–	–	300
Totals	157	3200	1800	1200	318	86	3300	3100	3100	1300	2000	500	2400	2100	11	146	185	800	3100	3300	3800	2200

Table 4*a*. *Dominant algae at Snakeholme Lock, June* 1931–*October* 1932, *in no./sq. mm.*

	1931						1932							
Date of collection ...	14. vi	30. vii	8. ix	10. x	15. xi	13. xii	24. i	6. iii	5. vi	23. vi	30. vii	29. viii	27. ix	22. x
Ref. no. ..	S 1	S 2	S 3	S 4	S 5	S 6	S 7	S 8	S 10	S 11	S 12	S 13	S 14	S 15
Cocconeis placentula	**600**	**800**	**62**	**400**	**16**	**8**	**600**	300	600	**1200**	**1600**	**1900**	**2200**	**1400**
Achnanthes minutissima	**500**	+	30	+	+	–	–	–	900	500	200	**2200**	+	+
A. lanceolata	+		–	+	+	–	–	+	+	+	–	+	–	–
Cymbella spp.	–	–	–	–		–	–	–	+	100	–	+	–	–
Gomphonema spp.	200	–	24		+	1	–	100	**2300**	600	100	**9200**	100	–
Nitzschia spp.	100	–	5	–	1	–	–	–	100	300	–	200	–	+
Other diatoms	100	–	11	–	–	1	100	–	100	+	+	1000	+	–
Characium sieboldi	–	–	–	–	–	–	–	–	–	200	+	100	100	–
Sporotetras pyriformis	+	–	–	–	–	–	–	–	900	100	+	+	–	–
Sphaerobotrys fluviatilis	–	–	+	+	–	–	–	200	100	–	100	200	100	+
Chaetopeltis orbicularis	100	+	–	–	–	–	–	100	200	300	100	100	300	300
Stigeoclonium spp.	200	–	2	–	–	–	–	100	600	200	200	400	400	100
Ulvella frequens	**800**	+	**96**	**400**	+	–	+	**800**	**3200**	**900**	**500**	**3500**	**800**	**500**
Other Chlorophyceae	100	–	+	–	–	–	–	–	800	600	+	100	–	100
Chamaesiphon spp.	–	–	–	–	–	–	–	200	700	–	+	100	–	+
Other Myxophyceae	–	+	–	–	–	–	–	–	100	–	–	–	–	–
Heterolagynion oedogonii	+	+	**77**	100	–	**28**	**300**	–	+	–	–	200	–	–
Totals	2700	900	313	1000	18	38	1000	1800	10000	5200	2900	20200	3800	2400

Table 4*b*. *Dominant algae at Snakeholme Lock. November* 1932–4. *in no./sq. mm.*

	1932	1933												1934			
Date of collection ...	26. xi	7. i	4 ii	11. iii	8. iv	6. v	22. vi	22. vii	19 viii	30. ix	29. x	2. xii	30. xii	27. i	17. iii	26. v	21. vii
Ref. no. ...	S 16	S 17	S 18	S 19	S 20	S 21	S 22	S 23	S 24	S 25	S 26	S 27	S 28	S 29	S 30	S 31	S 32
Cocconeis placentula	**1300**	**300**	**200**	**110**	**1400**	500	**2200**	**3900**	**1400**	**500**	**1300**	**1400**	**3**	5	**700**	**6100**	**5000**
Achnanthes minutissima	–	–	+	9		+	500	–	+	–	–	–	+	2	+	500	+
A. lanceolata	+	+	–	+	–	–	+	–	–	–	–	+	+	–	+	–	+
Cymbella spp.	–	–	–	–	–	–	–	+	–	+	–	–	–	–	–	+	–
Gomphonema spp.	–	+	+	4	300	**2200**	200	**600**	+	14	100	+	1	3	+	**3300**	**700**
Nitzschia spp.	+	+	+	3	+	+	–	–	–	6	+	+	–	–	–	–	–
Other diatoms	+	+	–	+	+	100	+	+	–	+	–	+	1	2	+	100	–
Characium sieboldi	–	–	+	–	+	–	–	–	–	4	+	+	–	–	–	–	–
Sporotetras pyriformis	–	+	–	–	400	900	–	–	–	–	–	–	–	–	–	–	–
Sphaerobotrys fluviatilis	100	+	+	–	500	200	100	100		–	+	+	–	–	–	**1900**	+
Chaetopeltis orbicularis	400	+	100	21	200	–	100	–	100	+	200	300	–	8	–	–	–
Stigeoclonium spp.	+	–	–	–	300	700	300	200	+	–	–	–	–	–	–	–	100
Ulvella frequens	**600**	**100**	**100**	**65**	**700**	**2900**	400	200	100	+	100	200	+	+	–	1200	200
Other Chlorophyceae	+	–	+	–	–	600	100	–	–	–	–	–	–	–	–	–	–
Chamaesiphon spp.	–	–	–	–		–	–	–	+	–	–	–	–	–	–	100	–
Other Myxophyceae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Heterolagynion oedogonii	+	+	+	+	–	–	–	–	–	79	+	200	1	**119**	**300**	–	–
Totals	2500	600	500	287	3900	8000	3900	5100	1800	680	1800	2200	6	145	1000	13400	6000

Table 5. *Dominant algae in West Beck at Snakeholme in no./sq. mm.*

	1932						1933											1934		
Date of collection ...	6. iii	8. v	29. viii	27. ix	22. x	26. xi	4. ii	11. iii	8. iv	6. v	22.vi	22.vii	19.viii	30.ix	29. x	2. xii	30. xii	27. i	17. iii	21. vii
Ref. no. ...	B 8	B 9	B 13	B 14	B 15	B 16	B 18	B 19	B 20	B 21	B 22	B 23	B 24	B 25	B 26	B 27	B 28	B 29	B 30	B 32
Cocconeis placentula	25	1100	10	8	200	300	200	200	200	1200	300	800	8	1	5	17	14	7	200	300
Achnanthes minutissima	1	+	1	1	100	100	+	+	+	800	200	+	3	+	1	3	2	1	+	+
Achnanthes lanceolata	+	–	–	+	–	+	+	+	+	+	+	–	–	+	–	–	1	1	–	+
Navicula spp.	–	–	+	+	–	+	+	+	+	+	100	–	–	–	–	+	1	–	+	+
Cymbella spp.	–	+	–	+	+	+	+	–	+	+	+	–	–	–	+	+	+	1	+	100
Gomphonema spp.	–	+	+	+	+	+	+	+	+	500	+	+	–	+	1	–	–	–	+	+
Nitzschia spp.	+	+	+	+	+	+	+	+	+	+	+	+	–	–	+	–	–	1	–	+
Other diatoms	–	+	–	+	+	+	+	+	100	+	300*	100*	+	–	+	–	–	–	+	+
Characium sieboldi	–	–	+	+	+	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Sphaerobotrys fluviatilis	–	+	–	–	+	–	–	–	+	+	+	+	–	–	–	–	–	–	–	–
Chaetopeltis orbicularis	–	–	+	+	+	–	+	+	+	–	+	+	–	–	–	–	–	–	–	–
Stigeoclonium spp.	–	–	–	–	–	–	–	–	+	+	100	+	1	–	–	–	–	–	–	–
Ulvella frequens	+	100	13	5	100	+	+	+	100	300	100	+	3	+	4	8	8	1	+	+
Other Chlorophyceae	–	–	4	+	+	–	–	–	–	+	+	–	1	–	+	–	–	–	–	–
Chamaesiphon spp.	–	+	–	–	–	–	–	–	+	+	+	–	–	–	–	2	3	+	600	–
Other Myxophyceae	–	–	–	–	–	+	–	–	–	–	–	–	1	–	–	–	–	–	–	+
Heterolagynion oedogonii	+	–	+	5	+	+	+	+	–	–	–	+	1	5	14	30	69	28	–	–
Totals	27	1300	30	20	400	400	200	300	400	3000	1200	900	17	7	25	64	99	40	800	500

* Amphora ovalis.

This community of algae, dominated by *Cocconeis placentula* and *Ulvella frequens*, together with other Chaetophorales (for species see appendix), is very common and widely distributed and has been found under the following circumstances:

(*a*) In calcareous waters which although unpolluted contain an appreciable quantity of dissolved salts. Such are parts of the Itchen, Test, Bristol Avon, Hampshire Avon, Skerne and Lark.

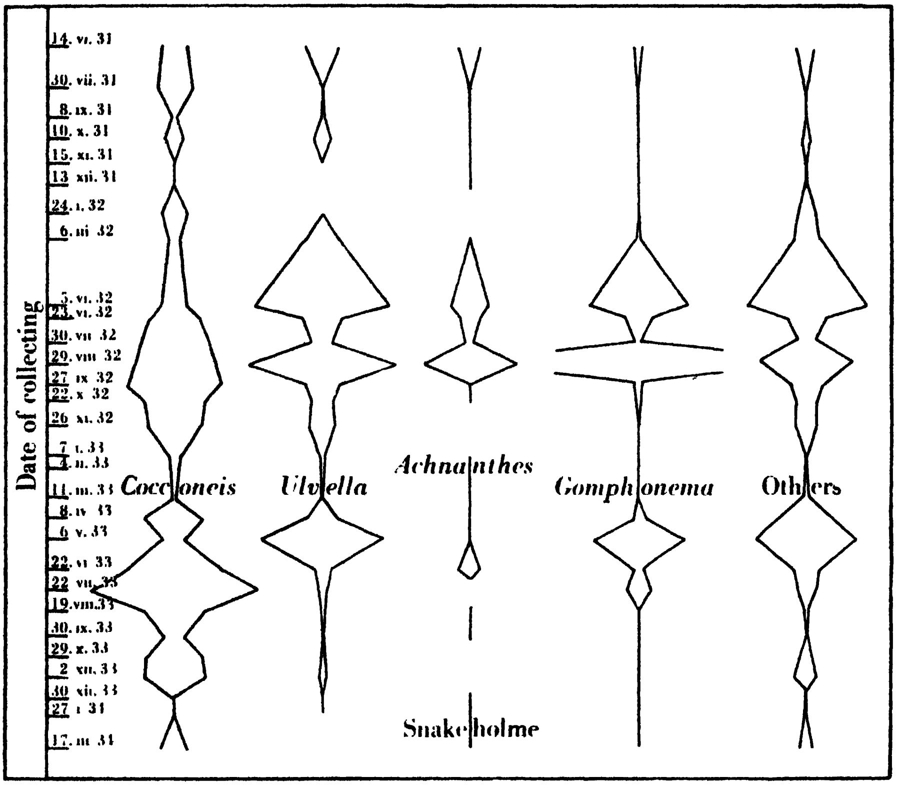

Fig. 1. Diagram of algae in no./sq. mm. at Snakeholme Lock.

(*b*) In both calcareous and mildly calcareous waters that have been polluted by organic matter but have recovered and still contain a plentiful supply of dissolved salts. Examples are the Tees in places immediately below the small sewage outfalls of the upper river and the lower Tees below the confluence of the Skerne at Croft in which stretch the water is both polluted and calcareous.

(*c*) In certain cases in non-calcareous waters that have been polluted with organic matter or contain a plentiful supply of mineral salts. The Balder, a tributary of the Tees and certain parts of the New Forest streams are examples.

The relevant characters of the Hull are a temporary hardness of 18 parts/100,000 $CaCO_3$, high ammonia, nitrate, organic matter and solids in solution

Table 6. *Mean no./sq. mm. of algae in river Hull*

	Driffield	Whinhill	Snakeholme	West Beck
Summer	2600	2200	4600	600
Winter	100	300	800	100

Table 7. *Mean no./sq. mm. of algae in certain places*

	Test	Itchen	Hants. Avon	Bristol Avon	Tees
Unpolluted	5600	6200	7300	8,600	3900
Polluted	—	—	—	23,700	6800

especially at Whinhill, generally mild pollution at the places sampled and no current.

In the Tees it was suggested that the *Cocconeis-Ulvella* community showed a relationship, not to the current nor the calcium content of the water but to the organic pollution. With this hypothesis the Hull falls into line. It was concluded also that the community in the Tees was related to the mineral salts derived from the organic pollution rather than from the organic matter itself but this fact does not help much since there are numerous salts derived from organic pollution. Of these, nitrates and phosphates have been extensively studied and though they are undoubtedly of great importance it must not be overlooked that many other compounds may influence the growth and distribution of algae. The chemical data for the Hull are very meagre, but, as there is pollution both by sewage and gasworks and nitrates are plentiful, there appears every reason to suppose that the other compounds such as phosphate and sulphate are also common.

The above remarks apply to *Cocconeis* and to its associates *Ulvella frequens*, *Stigeoclonium* spp. and *Sphaerobotrys* that have been usually found in the same community. Another alga, often codominant in the community is *Chamaesiphon*, and this is only rarely seen in the Driffield Canal and no suggestion to the reason of its rarity can be made. It is seen in quantity at times in the West Beck.

The *Cocconeis-Ulvella* community may be found in either soft or hard waters. It is a reasonable supposition that certain algae that do not occur under any circumstances in soft water may be found in hard waters. Such a list of algae was given for the Tees (Butcher *et al.* 1937) but further research has shown that this must be modified. It will be shown in a later paper that the algal growths in the unpolluted non-calcareous waters include algae hitherto never observed in hard waters, but a community associated with unpolluted hard waters has not been observed. Perhaps that is because no water has yet been examined that contains a high amount of calcium together with low concentrations of nitrate and phosphate.

Another alga to be commented on is *Heterolagynion oedogonii*. This is a small colourless member of the Chrysophyceae and it seems to become

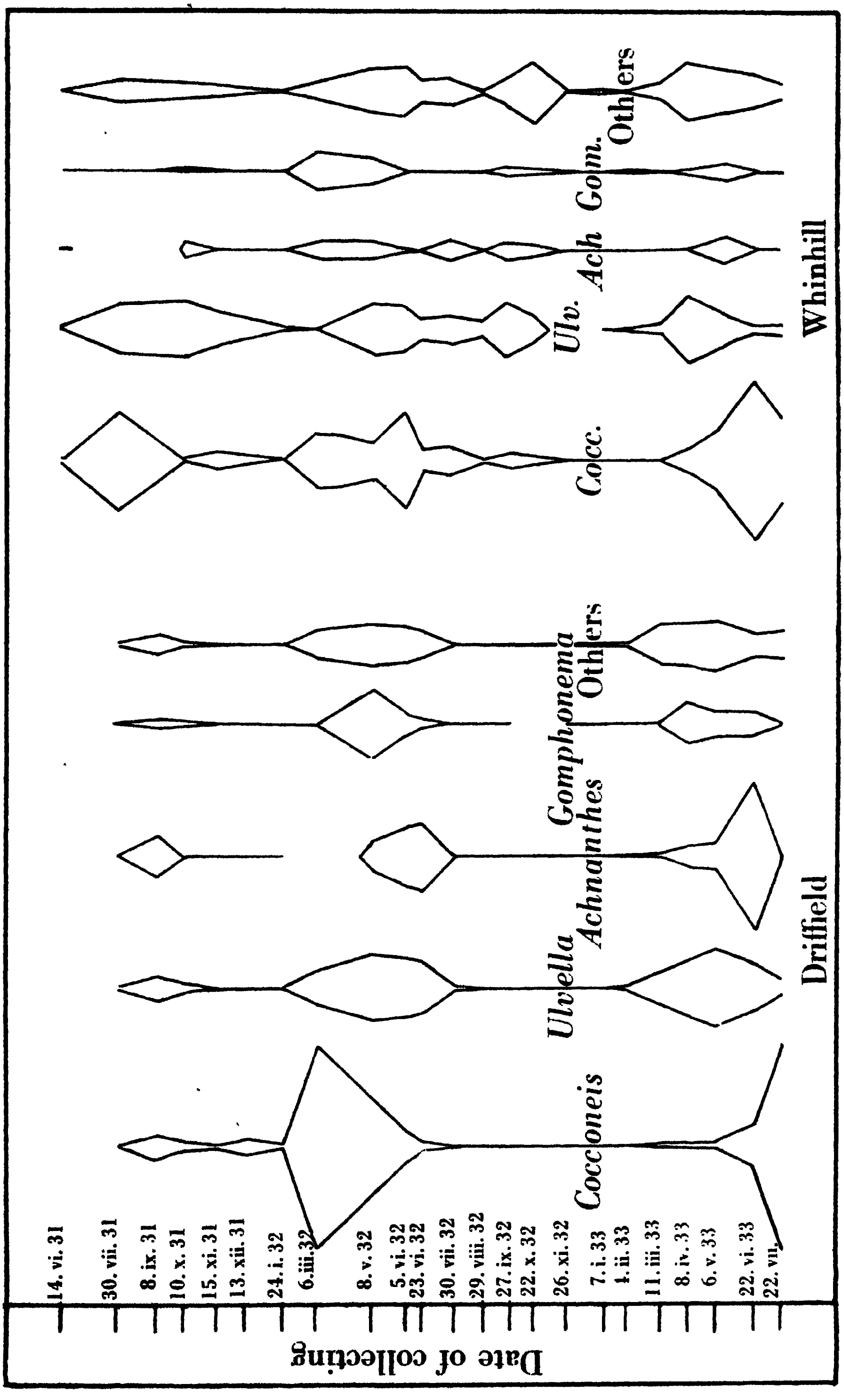

Fig. 2. Diagram of algae in no./sq. mm. at Driffield and Whinhill Locks.

plentiful only when the light intensity is low as, for example, when the water is turbid or in the winter. At such times other algae are rare.

Certain algae which are rare or unnoticed elsewhere are common in the Hull and in every river so far examined the same peculiarity has been noted. The species involved here are *Gomphonema longiceps*, *Characium seiboldii*, and undescribed species of *Chaetopeltis* and *Dermocarpon*.

DIFFERENCES IN ALGAL GROWTHS AT THE THREE STATIONS

If a table is constructed of the mean total and percentage composition of the commonest species at each station it will be seen that there are no striking differences between any of them. In all cases during the summer *Cocconeis* is dominant, ranging from 27 to 49% of the total, and *Ulvella* subdominant with 15–27% in the canal stations. The interrelation of *Achnanthes minutissima* and the Chaetophorales generally may also be noted. The former is commonest at Driffield above the sewage and in the West Beck where there is no sewage, while the quantity and subdominance of the Chaetophorales shows a marked increase after the sewage effluent has entered the canal. A similar tendency for *Achnanthes* to become less frequent and the Chaetophorales to increase has been noted in other cases of organic pollution.

The average figures are so much alike that it seems reasonable to conclude that the conditions for the development of the *Cocconeis-Ulvella* community were present throughout the river system and were not appreciably modified by the organic matter derived from the sewage that enters below Driffield Lock. The comparative rarity of *Chamaesiphon* in the canal has also been noted. The fact that it is occasionally common in the West Beck might indicate that it prefers the more quickly moving water. Further light on this point will be produced when discussing the algal growth of the river Itchen.

No reason can be assigned for the consistently low amount of growth at Driffield in the later summer of 1932 especially as there is no evidence of a depression in the numbers at Whinhill. It may have been due to some local factor such as the shading of the water where the slides were submerged, to the browsing activities of the fauna or possibly to the discharge of an effluent into the canal which had an unfavourable reaction on the growth of algae.

It is curious that although this station is above the sewage discharge, at certain times sewage fungus is abundant. It was common in July 1931 when a polluting discharge is known to have come from the local gas-works and also from July to October 1932 during the abnormal period of low growth above referred to. During the latter period however, no high values of ammonia such as one would expect with a discharge of gas liquor, were recorded.

In any case this period is clearly abnormal and if it were omitted, the mean growth at Driffield would be 3600 algae/sq. mm.

SEASONAL VARIATION

Since so many series of collections of algae taken at regular intervals show a definite periodicity it is generally accepted that, with both plankton and sessile algae, variation with the season, and therefore with physical and meterological conditions, is a general rule. It is therefore interesting to record a case where, except for the marked difference in the numbers between summer and winter collections, no seasonal variation is apparent. In the Hull the *Cocconeis-Ulvella* community is dominant throughout the year though in varying quantity from month to month. The diagram on p. 217 shows a series of peaks and depressions for each of the dominant species considered, but these come at very irregular intervals which may be termed spasmodic rather than periodic.

Monthly averages in no./sq. mm. of the dominant algae of the three canal stations added together show maxima as follows:

For *Cocconeis* May and July, for *Achnanthes minutissima* June and August, for *Ulvella*, *Gomphonema* and the total growths May and August. When referred back to the annual cycle of events at each station, however, all these maxima seem to be due to a single large collection in one year and not to a consistently recurring maximum under certain obvious conditions. The only point that is really consistent is that in the Hull, as in the Tees and the Bristol Avon, May is the most usual month of maximum growth.

The justification for stating that there is no marked periodicity in the algae lies in the fact that there is no sudden increase in one or two species followed by an equally marked decrease such as is shown by *Navicula viridula* in the Bristol Avon, by *Ulothrix zonata* or by *Cladophora glomerata* in the Tees.

The only species that suggests a periodicity is *Heterolagynion oedogonii* which appears more commonly in the winter than the summer.

This same lack of seasonal variation has been observed on the Hampshire Avon, the Itchen and the Test. These are all rivers fed by chalk springs where floods are small and in which all the substances considered to be essential for growth and development are apparently abundant and can rarely become a limiting factor. This may however be a chance co-relation though it does support the now generally accepted opinion that chemical factors play an important role in determining algal growths and development.

SUMMARY

The algae that grow on submerged glass slides were collected at four places on the river Hull over a period of 2½ years.

The Hull is a canal and the water is hard, mildly polluted by sewage and contains a plentiful supply of dissolved salts.

The number of algae growing on the slides is rather less than what is found in other calcareous waters but more than in non-calcareous waters.

The dominant algae are *Cocconeis placentula* and *Ulvella frequens*. This community has been found in rivers in which the one character in common seems to be a plentiful supply of nitrates and other mineral salts. No community characteristic of hard waters can be seen.

There is no seasonal variation and this may be because nutritive salts are always superabundant.

The author wishes to express his best thanks to Mr N. C. Akers of Hornsea who collected all the slides for three years and without whose assistance this work could not have been completed.

APPENDIX

List of algae found during 1931-3 *in the river Hull*

CHLOROPHYCEAE	
Palmellaceae	
Sporotetras pyriformis Butcher	Frequent at times
Chlorococcaceae	
Characium sieboldi A. Br.	Frequent
Oocystaceae	
Sphaerobotrys fluviatilis Butcher	Frequent
Selenastraceae	
Ankistrodesmus falcatus (Corda) Ralfs	Rare
Coelastraceae	
Scenedesmus bijugatus (Turp) Kütz.	Rare
S. obliquus (Turp.) Kirch.	Rare
Ulotrichaceae	
Ulothrix aequalis Kütz.	V. rare
U. zonata (Webb and Mohr) Kütz.	Infrequent
Cladophoraceae	
Cladophora glomerata Kütz.	Common at times
Chaetophoraceae	
Stigeoclonium farctum Berth. var. anglicum Butcher	Frequent
St. lubricum Kütz.	Rare
St. nanum (Dillw.) Kütz.	Uncommon
St. tenue Kütz.	Common
Ulvella frequens Butcher	Dominant
Coleochaetaceae	
Coleochaete scutata Breb.	V. rare
Chaetopeltidaceae	
Chaetopeltis orbicularis Berth.	Frequent
? Chaetopeltis sp.nov.	Frequent
Oedogoniaceae	
Oedogonium spp.indet.	Infrequent
Desmidiaceae	
Closterium acerosum (Schr.) Ehrb.	V. rare
Vaucheriaceae	
Vaucheria sp.	V. rare
BACILLARIOPHYCEAE—DIATOMS	
Melosira varians Ag.	Infrequent
Diatoma vulgare Bory	Frequent
Fragilaria capucina Desm.	V. rare
Synedra ulna (Nitzsch.) Ehr.	Frequent
S. tabulata (Ag.) Kütz. (affinis)	Rare
Eunotia arcus Kütz.	V. rare
E. gracilis (Ehr.) Rabh.	V. rare

Cocconeis placentula Ehr.	Dominant
Achnanthes minutissima Kütz.	Subdominant
A. lanceolata Breb.	Common
Rhoicosphenia curvata (Kütz.) Gr.	Common
Navicula cryptocephala Kütz.	Infrequent
N. gracilis Ehrb.	Infrequent
N. rhyncocephala Kütz.	V. rare
N. menisculus Schum.	Infrequent
N. viridula Kütz.	Infrequent
Cymbella cistula (Hempr.) Grun.	V. rare
C. ventricosa Kütz.	Frequent
Amphora ovalis Kütz.	Rare
Gomphonema acuminatum Ehrb.	Abundant
var. brebissonii Kütz.	Abundant
var. coronatum (Ehrb.) Sm.	Abundant
G. constrictum Ehrb.	Frequent
G. longiceps Ehrb. var. subclavata (Gr.) Hust.	Dominant
G. parvulum Kütz.	Frequent
G. olivaceum (Lyng.) Kütz.	Frequent
Nitzschia dissipata (Kütz.) Grun.	Infrequent
N. amphibia Grun.	V. rare
N. palea (Kutz.) W. Sm.	Common
N. subtilis Grun.	Rare
N. acicularis W. Sm.	Rare
CHRYSOPHYCEAE	
Heterolagynion oedogonii Pascher.	Frequent
MYXOPHYCEAE	
Dermocarpa sp.nov.	Infrequent
Chamaesiphon incrustans Grun.	Frequent
C. regularis (Fritsch) Geit.	Infrequent
Phormidium molle (Kütz.) Gom.	Rare
P. tenue (Menegh.) Gom.	V. rare
P. foveolarum (Mont.) Gom.	V. rare

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THE RECORDING OF STRUCTURE, LIFE FORM AND FLORA OF TROPICAL FOREST COMMUNITIES AS A BASIS FOR THEIR CLASSIFICATION

By P. W. RICHARDS, A. G. TANSLEY and A. S. WATT

(*With two Figures in the Text*)

At the Annual Meeting of the British Ecological Society in January 1938, Dr J. Burtt Davy read a paper on "The classification of tropical woody vegetation types", with the object of obtaining constructive criticism from the Society. As a result of the discussion which followed, a committee of three (the authors of the present paper) was appointed to examine and report on the subject. The Committee carefully considered Dr Burtt Davy's paper published, under the title mentioned, by the Imperial Forestry Institute as Institute Paper No. 13, Oxford, 1938, and duly reported to the Council of the Society. At a recent meeting this Report was approved and adopted by Council, which accepted an invitation to publish it, with appropriate modifications, as an Imperial Forestry Institute Paper[1] and ordered that it should also appear in *The Journal of Ecology*.

The present paper contains the substance of the Committee's Report. Most of it is unaltered, but the introductory portion has been rewritten for publication.

There is an urgent demand for stabilization of the nomenclature of tropical forest vegetation, on the part of Conservators and other Forest Officers, in order to avoid the confusion and misunderstanding that result from different officers calling the same things by different names and possibly different things by the same name. Dr Burtt Davy's essay on the classification of tropical woody vegetation types, above referred to, is a praiseworthy effort to meet this need. But it must be recognized that a natural classification of any set of phenomena can only be made when our acquaintance with the facts on which a classification can be based has reached a fair degree of completeness. In the present inadequate state of our knowledge of tropical woody communities no classification can be other than provisional, and Dr Burtt Davy claims no more for his effort. The authors certainly do not possess knowledge that would enable them to replace it by anything which they would consider a satisfactory classification, nor can such knowledge be obtained from existing publications.

The use of mixed criteria, largely but not wholly based on habitat—wetness and dryness, evergreen and deciduous habit, stature and life form, altitude, and sometimes the systematic position of dominants—must lead to the setting up of "formations" which cannot be regarded as of equivalent status or value.

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[1] Institute Paper, No. 19, Oxford, 1939. Price 1*s*.

The classification professes to deal only with "climax types", but there is the fundamental difficulty of drawing a line between true seral communities and "edaphic climaxes". To draw a valid distinction between these depends on the possibility of making a correct judgement between vegetation undergoing continuous change and relatively stable vegetation occupying a more or less permanently differentiated habitat, and this is often not possible by immediate direct observation. For practical purposes no doubt it is essential to include all *relatively* permanent types with which the forester has to deal, but even when such types have been recognized they cannot be rationally classified on the criteria employed without understanding their status, and this is just what the working forest officer does not know, and usually has no means of ascertaining in the time at his disposal. All that can be done on these lines is to arrange in some sort of order the types of forest community that have been distinguished and given names in different parts of the tropics on the basis of the most various characters. Some are doubtless natural types, though of varying status, and will eventually fall into their proper places in a natural scheme. Others are unsatisfactory both in name and definition. The equation of African and Indian types is probably premature, at least until someone has made a thorough comparative examination of the forests in the two continents.

Since we have nothing better to put in its place it would not be helpful to criticize Dr Burtt Davy's scheme in detail. As a result of his years of work on tropical forest trees at the Imperial Forestry Institute, and of his personal acquaintance with both the eastern and the southern tropics of Africa, the author probably has a greater knowledge of African tropical forests as a whole than any other single individual. His courageous initiative in attempting to meet an urgent need has been widely welcomed, and African forest officers will probably do well to put his classification to the test of practical use. That is the surest way of revealing weakness and of paving the way for a future natural scheme.

The authors hold that such a scheme must be inductive, based on the structure, life form and flora of the communities themselves, not on mixed criteria which include necessarily vague characterizations of habitat. Existing knowledge is still inadequate for the construction of a natural classification. We are of opinion that Forest Officers should be encouraged and assisted to collect and record data on a uniform plan concerning the structure and other characters of the forests in which they are working. The correlation of such data would be greatly facilitated if they were filed at a central institution where they would be available for consultation and study. We suggest the Imperial Forestry Institute as a suitable location. Together with records already in existence an extensive series of such data would form, in our judgment, the only sound foundation for a future natural classification. At the same time we hold that increased opportunities for the study of modern methods of ecological observation and record should be given to undergraduates intending to pursue forestry as a career and to Forest Officers taking refresher courses when on leave.

Meanwhile the authors feel that the best contribution they can make towards laying the foundations of such a future system is to call attention to certain basic principles and to suggest the points of prime importance which forest officers should observe and record. Nearly all these points indeed are included in Dr Burtt Davy's *Appendix: outline list of facts to be recorded in field work*, pp. 76–85; but since this comprises no less than ninety-six separate topics, it is felt that field workers are likely to be deterred from attempting any systematic records of vegetational data by the immensity of the task suggested. It is important that first things should be put first. With Dr Burtt Davy's remarks on p. 76, and with his quotations from Salisbury on p. 77 of his paper we are in complete agreement.

METHOD OF APPROACH

An actual sample of forest to be studied in the field is best regarded in the first place as a particular example (sometimes called a "stand") of an *association* (dominated by two, several, or many species) or of a *consociation* (dominated by a single species), and characterized by the total *flora*, i.e. the whole collection of species present, though some species (sometimes called "*characteristic*") have a greater diagnostic or "indicator" value than others.

Note on "dominance". *Dominants* in the ecological sense are members of a plant community which have a determining or controlling influence on the rest of the vegetation belonging to it. The trees forming the main canopy of a closed forest are typical dominants of the community, since in their absence much of the subordinate vegetation—the lower layers of the forest—would not exist. The subordinate or lower layers may also have their own dominants (low trees, shrubs or tall herbs) which similarly contribute to the control of the vegetation below each corresponding layer. Wherever vegetation is dense the tallest plants of the whole community and of each layer will necessarily exercise this controlling influence because they reduce and modify the light reaching lower layers and also increase the stillness and humidity of the air. But the tallest plants of some complex communities are not necessarily controlling, for example when they are scattered or do not effectively reduce the light reaching lower layers. Thus the main controlling layer of the forest whose profile is shown in Fig. 2 (facing p. 234) is the comparatively low stratum of trees whose crowns are developed from about 20–40 ft. above the ground, rather than the much loftier but more scattered trees reaching 100 or 150 ft. And the trees of a savanna, which have little or no effect on the grasses, etc., that constitute the "field layer" are not the "true" dominants of the savanna. These are the tall grasses, etc., which do actually exercise a controlling effect on any plants of lower stature growing between them. Nevertheless the trees of a savanna are often spoken of as "dominants" because they are the tallest and most conspicuous plants present. It is better to use the term "physiognomic dominants" for the conspicuous trees which give "character" to the savanna, and since the tall grasses share in this "character giving" quality they are also "physiognomic dominants" as well as being "true" dominants of the field layer.

The silvicultural use of the term dominant differs from the ecological use. "Dominant" trees of a forest canopy are commonly defined by foresters as those whose crowns are more than half exposed to full illumination, while the crowns of "subdominant" trees are partly, but less than half, exposed to full light, and those trees whose crowns are wholly shaded are spoken of as "suppressed". This usage thus applies to the actual development of an individual tree, while the ecological use applies to layers of vegetation in their relation to, and effect upon, other layers. The discrepancy is unfortunate, but it is difficult to see how a description which is to be of ecological value can avoid the use of the term dominance in the ecological sense. It is therefore suggested that the expression "dominant (ecol.)" should be employed to make the distinction clear.

Isolated trees whose crowns rise above the general canopy are a constant feature of several types of tropical forest. They are clearly "dominant" in the silivcultural sense, but not in the ecological, since they can exercise no general controlling influence on the forest. The term "pre-dominant" has sometimes been applied to them, but since this term may be thought to imply a specially high degree of dominance, it is suggested that the term *emergent* may be used instead. "Emergent" trees may be considered collectively as forming an "extra" (discontinuous) layer above the general tree canopy.

A particular forest examined may be a typical example of an association or consociation, or it may deviate from the commonest type more or less widely, but the criterion is the presence of particular dominants and a particular flora.

Certain associations and consociations are found to agree in the *life forms* of their component species, especially of their dominants, though the species may be totally different. This agreement in life form indicates similarity of *essential habitat*, especially similarity of regional climate, and the associations showing such agreement may be put together in a larger unit—the *formation.* Within an area of uniform climate, however, edaphic or biotic factors may have been at work to prevent the development of the typical climatic vegetation, and here the essential habitat and the life forms of the dominants are immediately determined by these edaphic or biotic factors. Different associations and consociations which agree in life form so determined are called *edaphic* or *biotic formations.*

Formations of very well-marked life form are so strikingly and characteristically similar and are so obviously determined by similar climates, in whatever part of the world they may occur, that they have long been recognized as together forming distinct entities, which we may call *formation types.*[1] Thus the tropical forests in the high rainfall region of West Africa, of Central and South America, and of the Malay region, together belong to the formation type of tropical rain forest, and are composed of very similar life forms, though they show important differences between the different continents, and are best regarded as separate formations. Similarly with the deciduous summer forests of Europe and eastern North America, which are sufficiently differentiated to be treated as separate formations, but certainly belong to one formation type. When however we try to group intermediate and less well differentiated communities into formation types, or even into formations, we encounter many difficulties, and the task cannot be satisfactorily carried out until an extensive series of data concerning the structure and composition of a great many associations has been accumulated. It is the collection of these data and the characterization of the forest associations on the basis of their structure and composition that is the primary task of the student of forest vegetation, be he practical forester or ecologist, because without such knowledge no progress can be made either in scientific knowledge of the vegetation or in rational treatment of the forest.

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[1] This use of the term "formation type" we think better than Dr Burtt Davy's application of it to Schimper's primary division of land vegetation into Forest, Grassland and Desert, for which no special term is really needed.

THE UNIT TO BE STUDIED

Clearly it is first of all necessary that a definite name should be given to the particular sample of vegetation under investigation. The recognized name of a consociation is taken from the generic name of the single dominant, e.g. Rhizophoretum, from *Rhizophora*, one of the commonest dominant mangroves. An association is named from two (or sometimes three) dominants, e.g. the *Isoberlinia-Brachystegia* association. In many tropical forests, notably rain forest, the canopy may be formed of so many different species that it is quite impracticable to include them all in the name of the association, even when they are all known. It is sometimes said that such associations have no dominants, but in reality the species of the canopy are jointly dominant, for collectively they determine the conditions in which the undergrowth lives. It is only where the undergrowth present has little or no relation to the trees, as in many savannas, that the function of ecological dominance is confined to some lower layer, or, as in desert, may be absent altogether. When it is impossible to use the names of dominants in designating an association, either because they are very numerous or because they are absent, recourse must be had to the names of characteristic species, if necessary including characteristic species of subordinate layers. Associations should always be named from species present, not from a presumed formation to which the association belongs. In this way objectivity is obtained and possible mistakes and confusion avoided.

The following points should therefore be first recorded:[1]

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[1] The points suggested for record are numbered consecutively throughout. For convenience a separate list of the points, without explanations, is given on pp. 237–239.

Name and location.

(1) Name given to the community (from names of dominant or characteristic species).

(2) Popular or native name, if any.

(3) Exact location of the stand or sample examined.

Size and nature of samples studied:

(4) One or more sample areas, each of which it is suggested should not be less than an acre in extent. Additionally or alternatively a belt transect of a uniform area, length and breadth.

When a traverse or transect is made through a considerable extent of forest it is important that samples should be taken in homogeneous portions and separately described. When sample plots are selected in connexion with ordinary "working plans" there is every reason why these should be chosen for description.

(5) Altitude, exposure, aspect, slope.

STRUCTURE AND COMPOSITION

Description

Vegetation should be primarily characterized *by its own features*, not by habitat, indispensable as is the study of habitat for the understanding of its nature and distribution. It is the *structure* and *composition* of a plant community that we must first ascertain and record as the secure basis of all subsequent knowledge.

Structure

We may distinguish structure in the horizontal from structure in the vertical dimension, corresponding respectively with "spacing", and stratification or "layering". The canopy of a forest is either closed or open, and the constituent trees stand certain average distances apart, while a primary characteristic of all but the simplest communities is their stratification. The stratification of a forest may be sharply defined or ill-defined, but, except in rare cases where the forest consists solely of one layer of trees of uniform height and no undergrowth, there is always *some* stratification. The points to record are therefore

(6) Closed or open canopy: if open the approximate width of gaps or the approximate percentage of shaded and unshaded areas. The scale of density from 0 to 1 often used in forest records may be employed.

(7) Uniform or irregular spacing of trees: distances apart of the trunks: diameters of trunks of apparently mature trees of different species.

(8) General description of stratification: how far distinct strata or layers can be recognized: enumerate these.

The following names of layers in a complex, well-stratified forest such as rain-forest are useful: (*a*) Emergent tree layer or layers—discontinuous; (*b*) Dominant tree layer (canopy);[1] (*c*) Subordinate tree layer or layers; (*d*) Shrub layer; (*e*) Field layer or layers, (*e*, i) tall herbs, ferns or low shrubs, (*e*, ii) lower ferns, selaginellas or herbs; (*f*) Ground layer (mosses). Any or all of these except the dominant tree layer may be absent in some closed forests. It is important to note that layers are *spatial* characters, each consisting of species of approximately the same height, whose shoots are therefore in direct competition for space and light. Thus sapling or low trees may belong to the shrub layer, dwarf shrubs and seedling trees to the field layer.

(9) Separate description of each well-marked layer, with the range of height of its foliage above the ground. Where distinct layers are absent, general description of structure in the vertical dimension, with ranges of height of the various components.

(10) Societies, i.e. local aggregations of individuals of a species observed in any of the layers.

Besides the primary stratification of a forest the presence of climbers, especially woody lianes and epiphytes, may be important diagnostic features of the structure.

(11) Lianes, height to which they ascend; epiphytes (particulars of kinds of epiphytes, e.g. strangling figs, orchids, bromeliads, ferns, etc.): presence and frequency: distribution in height: distance from ground to which they descend.

Composition

(i) *Physiognomy and life form.*

The "physiognomy" or general appearance of a forest depends upon the stature, spread, and life form (in the widest sense) of the species composing it, primarily of the dominants or canopy species. Essential information about the life forms of these and other constituent species can be recorded even when the names of the species are not known. It is therefore desirable in the first instance to keep what may be called *life-form composition* separate from *floristic composition.*

Life forms of trees. Apart from the stature and general habit of a tree, a number of characters often present in certain tropical forests should be noted:

(12) Plank buttresses; stilt roots; pneumatophores ("breathing roots"), erect or "knee-shaped"; thorny trunks or branches, cauliflory, peculiarities of bark, succulent leaves or stems.

(13) Any special woody life forms present, e.g. palms or cycads, bamboos, rattans, pandanus.

Two of the most important general features of a life form are (*a*) whether it is evergreen or deciduous and (*b*) the size of the leaf. Leaf size is often an important index of habitat. The following records should therefore be made:

(14) Evergreen or deciduous: if mixed, percentages of each.

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[1] A continuous canopy may be formed only by a comparatively low layer. Cf. p. 226 and Fig. 2.

(15) If deciduous the season of foliation and leaf fall.

(16) Leaves simple or compound: if compound, pinnate or digitate, and approximate number of leaflets.

(17) A useful characterization of leaf size can be made by assigning the leaf to one of Raunkiaer's "leaf size classes" with the aid of the accompanying diagram (Fig. 1). In compound leaves it is the single leaflet that is to be assigned to its size class, but the overall measurements of the whole leaf should also be included in the record.

The leaf characters (14)–(17) should be recorded for each tree layer separately, and also for the shrub layer if present. If time is not available for full records the emergents (if present) and the canopy dominants are the most important, because their crowns are fully exposed to the regional or local climate.

Note. To record the leaves of every kind of tree and shrub present in a forest containing many species will probably be quite out of the question. The observer may content himself with records of the more abundant and typical species, including also any species which depart widely from them. He should never neglect leaf size altogether.

(18) *Life forms of field and ground layers.* General notes on the types present, their frequency and gregariousness, e.g. abundance of tall herbs, ferns, selaginellas, or mosses.

(19) *Periodicity of field layer*: seasonal dying down of any subordinate layer or important constituents: annual plants, if any.

Reproduction. (20) Seed production of important trees: amount, kind of seed, mode of dispersal, if any. Relation between number of seedling trees and seed-bearing parents. Ability of tree seedlings to endure shade.

(21) Observations on vegetative propagation of particular trees and shrubs.

(ii) *Floristic composition.*

The total flora of a forest is as it were the "building material" of its vegetation. The trees are the primary objects of interest to the forester, and in the first instance every effort should be made to identify the species of tree present. When a species is recognized with certainty its name will naturally be used in the foregoing records relating to that species. But since the flora of tropical forests is still very incompletely known, the method of collecting adequate herbarium specimens of unknown or uncertain trees, designating them by an attached number, and forwarding them to the appropriate herbarium for identification (or, with undescribed species, for description) is indispensable. The corresponding number should then be used for records of the composition of the different layers of the forest, of leaf characters, and of the other features recorded. In this way a great deal of valuable information about a given forest can be recorded and systematized before the species are properly named, or even before they are described in the herbarium, though comparison with the flora of other forests studied by different workers cannot

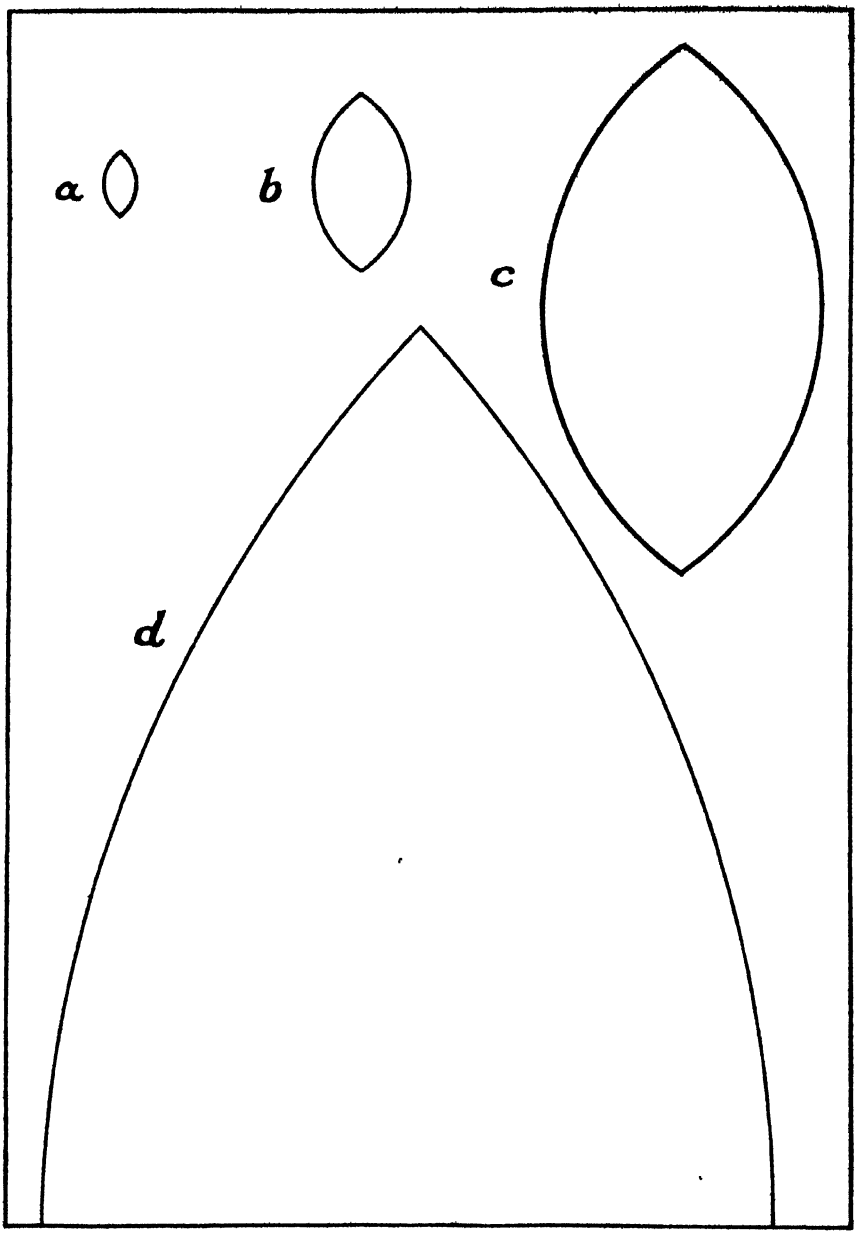

Fig. 1. Limiting sizes of Raunkiaer's six leaf size classes.

Leptophyll, less than *a* (25 sq. mm.).
Nanophyll, between *a* and *b* (225 sq. mm.).
Microphyll, between *b* and *c* (2025 sq. mm.).
Mesophyll, between *c* and 2*d* (18,225 sq. mm.).
Macrophyll, between 2*d* and 8 times the area of the whole diagram (164,025 sq. mm.).
Megaphyll, more than 8 times the area of the diagram.

The size class of a leaf can usually be rapidly determined by eye on comparison with the diagram. The limiting size between two successive classes is 9 times the area of the limit next below in the series.

of course be made till the species are known by universally recognized names. It is important that the forest officer should realize that he can collect all essential data before valid names have been given to the species he deals with. Native names of trees, if the same name is consistently applied by forest natives, are often useful and should always be recorded.

Citation and reliability of names. Since accuracy and precision of naming species is of vital importance to the building up of exact knowledge of forest composition, the following points should be borne in mind.

When identifications are based on specimens collected, the herbarium in which the species are deposited should be stated and the collecting number of the specimen given in brackets after the scientific name of each species. Where the identifications are made by the observer himself with the help of a flora, the name, author and edition of the flora should be stated.

The reliability of an identification will necessarily vary with the grounds on which it is based. Thus (*a*) the species may not have been collected by the observer, and the identification merely based on a vernacular name, the corresponding scientific name being obtained from a check list and originally given to a specimen collected in a distant locality: (*b*) the species may have been collected in the same locality but not from the same stand: (*c*) the species may have been actually collected in the stand described. It is clear that the reliability of the identification increases from (*a*) to (*c*), but that even in (*b*) and (*c*) it depends on the observer's judgment of identity between the specimen collected and all the individuals referred to under the name in the stand described. The "degree of reliability" of the name may be indicated by a convention such as that used by Richards (*J. Ecol.* **27**, 1939, p. 53 note).

(22) List of all species distinguished, whether their proper names are known or not; *each layer of the forest should be listed separately.* Where there is a number of species present which the observer is unable to separate and identify either by name or number the fact should be noted.

It is often useful and possible to add to the name or number of each species a symbol representing the frequency of its occurrence in the sample described. Symbols in general use are: *a* = abundant, *f* = frequent, *o* (or *occ.*) = occasional, *r* = rare, *l* = local. These symbols necessarily represent subjective estimates of frequency and are thus subject to errors due to the "personal equation", but they are still useful, especially when time does not permit of numerical counts. Actual counts on which percentages of the species present can be based, especially counts of the larger trees, should be made whenever possible. When a species which might be expected to be present (from its occurrence in other forests known to the observer) is conspicuous by its absence, its name may be added with the symbol *abs.* = absent. [This is better than O = absent, because of possible confusion with *o* = occasional.] Absence of particular species may be an important diagnostic character of the community, just as may the presence of particular species which are absent from other communities. Notes should be added to the names of any species which experience shows to have a high diagnostic or "indicator" value.

The forest officer may be unable to afford time for the study required to separate and list the species of the field and ground layers, since proper attention to the trees is sufficiently exacting. He may even have to neglect the smaller trees. But he should not ignore the existence of the lower layers of the forest, since they are integral parts of the vegetation, and he should always write careful general notes about them.

Note on the study of community structure. Full records under the preceding numbered heads should give a good picture of the structure of a given forest community, indispensable as a basis for the classification of forest types. The points given have been restricted to those necessary for an outline of essential structure and not too time-consuming.

Much closer study is of course possible and valuable. The most useful technique for such closer study of the tree layers of a sample of forest is its representation by a profile diagram drawn to scale, of which an example is shown in Fig. 2.

A narrow strip of forest is marked out with stakes and ropes. A convenient width is 25 ft., but the width should be varied according to the density of the stand: the length should be not less than 200 ft. in high forest. Small undergrowth less than 15 ft. high is cleared and removed from the strip: if the trees are very dense, it may be necessary to remove all trees less than 25 ft. high. The positions of all the remaining trees on the strip are then mapped and as this is done a number is assigned to each tree and written on a blaze on its trunk. The trees are now felled in a carefully selected order, beginning with the smallest. For each tree felled the following data should be recorded: name (vernacular and scientific, if known) and/or distinctive number, diameter at breast height, total height, height to base of lowest branch (neglecting small twigs on the trunk, etc.), height to lowest leaves (neglecting those on small twigs), spread of crown (this can usually only be roughly measured). From these data, a profile diagram (elevatión) can be drawn to scale. See Fig. 2 (cf. Richards, *J. Ecol.* **24**, 1936, Figs. 2 and 3, p. 10; and *ibid.* **27**, 1939, Figs. 4 and 5, p. 18). Herbarium material should be collected from each species, whether in flower or not, and to this the distinctive number should be firmly attached. Other data than those mentioned may be recorded, if desired, e.g. height and distribution of epiphytes.

Such a graphic representation of forest structure gives concreteness to the description, and furnishes precise data, enabling essential points of structure to be quickly appreciated.

Photographs of forest vegetation may also be very valuable. Those published vary very much in quality and the greatest care is necessary if useful pictures are to be obtained.

Use of accurate data concerning community structure and composition. The facts of community structure, life form, and leaf size are the only sound basis for a future natural classification of forest associations and consociations, which may then be grouped according to their *vegetational* affinities into formations and formation types; and these will be found to correspond with the broad features of their habitats, primarily climatic, but also sometimes edaphic or biotic. But the associations and consociations, characterized by specific dominants and flora, will themselves be found to show many variations,

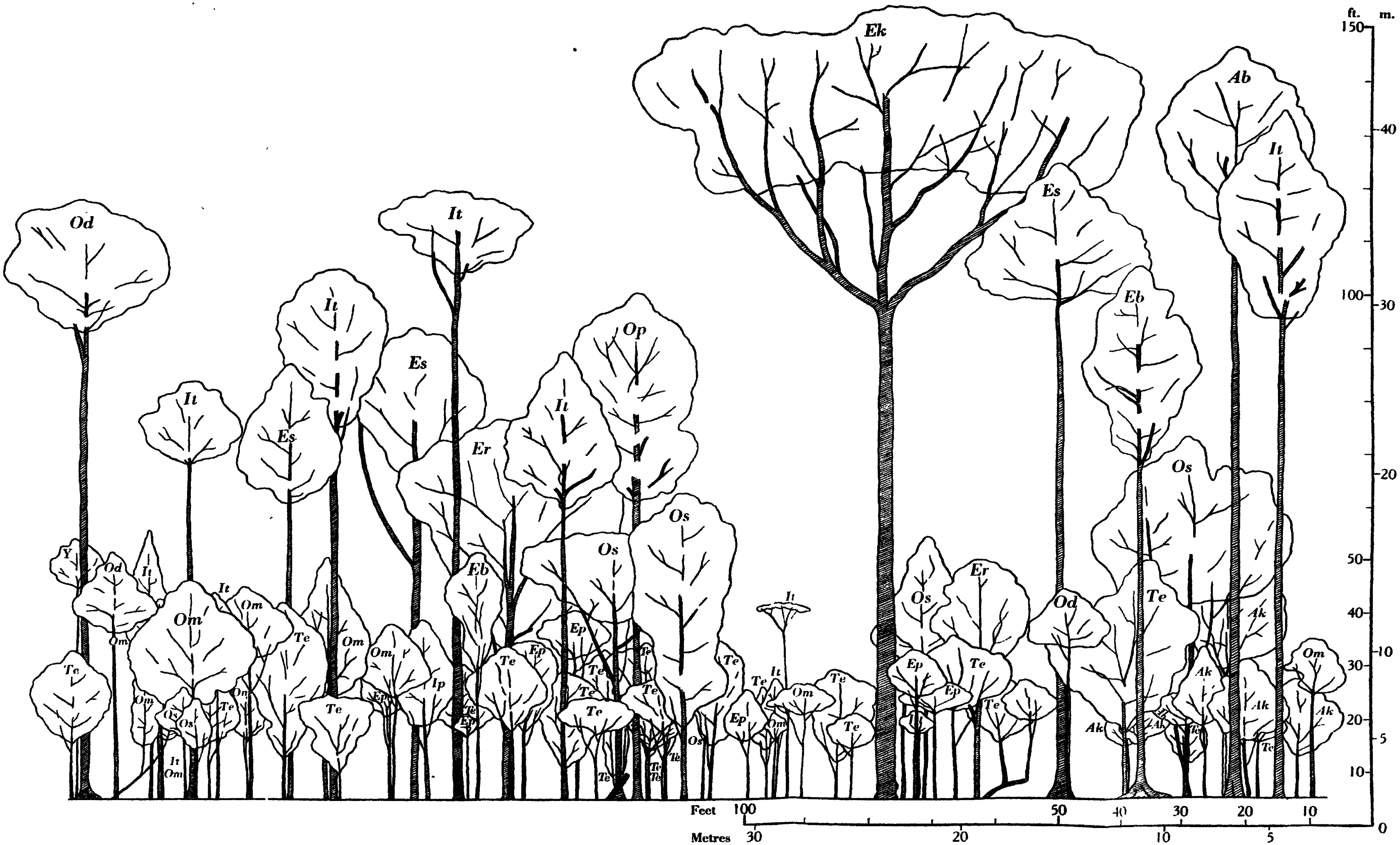

Fig. 2. Profile diagram of primary Mixed Rain Forest C.F.P.I., Shasha Forest Reserve. The diagram represents a strip of forest 200 ft. (61 m.) long and 25 ft. (7·6 m.) wide. The position, diameter at breast height, total height, height to the first branch, lower limit and spread of the crowns of the trees are based on measurements and drawn strictly to scale. As a convention the crowns are drawn compact and dense, though in fact they very rarely are so. All trees 15 ft. (4·6 m.) high and over are shown. The letters indicate the vernacular names of the species. (From P. W. Richards, Ecological Studies on the Rain Forest of Southern Nigeria, I. The Structure and Floristic Composition of the Primary Forest. *J. Ecol.* **27**, 1939. Fig. 4, facing p. 18.)

largely depending on minor differences of habitat and characterized by the frequency, presence or absence of certain species, including the presence or absence, development and size of particular trees. It is this last feature which may often determine whether exploitation is worth while or not.

An indication may be given of the way in which the life form and structure of forest communities would be used to group them into formations, though an actual detailed classification is premature. A primary division (omitting shrub communities) would be into

A. *Forest proper*, with shade-bearing undergrowth, i.e. the subordinate layers determined by the tree canopy.

B. *Savanna* (in the wide sense) with no shade-bearing undergrowth, i.e. the subordinate layers not determined by the presence of trees.

The forests proper would be divided into predominantly evergreen and predominantly deciduous, perhaps with an intermediate "mixed" group, and these again according to the complexity of their stratification. The evergreen forests at least can be naturally arranged according to the average leaf size of the trees, which corresponds with climate. In Savanna the field layer is typically dominated by tall grasses in tropical Africa, and often by undershrubs in Australia. Whether the trees are scattered or in clumps (true Savanna) or whether they form a continuous canopy (Savanna forest) the trees have little effect on the field layer.

A classification on these lines would probably correspond very closely with habitat: the advantage is that it is based on easily observed and measurable phenomena. When we say that a forest is dominated by evergreen trees with leaves of a certain average size, and that it shows such and such stratification, we are making perfectly definite and easily verifiable statements. When we say that it is "wet" or "dry" we are making vague statements to which no quantitative values can be attached without long-continued research. Thoroughgoing study of the habitat and of its effect on the vegetation is of course essential to ecological science, but the working forest officer has rarely time to undertake it. He can however collect and record certain habitat data which are of considerable value, and these should be added to his descriptions of community structure and composition.

HABITAT

In this we include all the factors of the environment—climatic, physiographic, edaphic, and biotic—which act effectively on vegetation. We do not however know, to begin with, which environmental factors are really effective and which are not, and the ecologist must therefore cast his net wide. But experience has taught us that certain factors are always important, and it is the relevant data in regard to these that the forest officer should collect as far as he can.

Climate. The following data should be recorded from the nearest meteorological stations, with a note as to the distance from the forest described and any physiographic difference likely to introduce differences between the climate of the station and of the forest, e.g. differences of altitude, exposure or protection.

(23) Mean temperature of hottest month.
(24) Mean temperature of coldest month.
(25) Absolute maxima and minima recorded.
(26) Mean rainfalls of separate months.
(27) Length of dry period or periods: mean number of consecutive days without rain or with negligible rain.
(28) Any corresponding data obtained from the forest itself or its immediate neighbourhood.
(29) Prevailing winds and periodic or seasonal winds of special significance.

Soil and Subsoil. (30) Kind or kinds of rock.
(31) Kind of soil (e.g. sand, gravel, loam, clay, etc.): humus.
(32) Surface litter: nature, depth.
(33) Soil profile, with measurements of horizons distinguishable: colour, texture: rooting depths.
If there is opportunity for mechanical and chemical analysis, samples (with depths carefully recorded) should be collected for this purpose.
(34) Soil-water relations: erosion, run off, depth of water-table and its variations at different seasons.

History of the area. (35) Has the area now occupied by forest ever been cultivated? Any available details about the nature of such cultivation and time of abandonment.

Biotic factors. (36) Tree felling.
(37) Shifting cultivation, with details of periods and methods.
(38) Grazing: animals grazed: effects observed.
(39) Any observable effects of grazing or trampling by wild animals.
(40) Presence or absence of termites: any observable effects on the vegetation.
(41) Burning: accidental or intentional: reasons for, and details of intentional burning: effects.

SUCCESSION

(42) Apparent stability or instability of the forest. If it is obviously changing, indications of the community into which it is changing. Observations on any communities preceding the development of the existing forest.
Species which are invading or increasing: species that are diminishing in number of individuals or disappearing. Observed or suspected causes of change in composition. Any concomitant changes in soil.

LIST OF POINTS SUGGESTED AS THE MOST IMPORTANT FOR RECORD BY FORESTRY OFFICERS

Name and location.

(1) Name given to the community (from names of dominant or characteristic species).

(2) Popular or native name, if any.

(3) Exact location of the stand or sample examined.

Size and nature of samples studied.

(4) One or more sample areas, each of which it is suggested should not be less than an acre in extent. Additionally or alternatively, a belt transect, length and breadth.

(5) Altitude, exposure, aspect, slope.

STRUCTURE AND COMPOSITION

Structure.

(6) Closed or open canopy: if open the approximate width of gaps or the approximate percentages of shaded and unshaded areas.

(7) Uniform or irregular spacing of trees: distances apart of the trunks: diameters of trunks of apparently mature trees of different species.

(8) Description of stratification: how far distinct strata or layers can be recognized: enumerate these.

(9) Separate description of each well-marked layer, with the height of its foliage above the ground. Where distinct layers are absent, general description of structure in the vertical dimension, with ranges of height of the various components.

(10) Societies, i.e. local aggregations of individuals of a species observed in any of the layers.

Physiognomy and life form.

(11) Lianes, heights to which they ascend: epiphytes, distribution and frequency, particulars of kinds of epiphyte—orchids, bromeliads, ferns, strangling figs., etc.: distribution in height, distance from ground to which they descend.

(12) Plank buttresses: stilt roots, pneumatophores ("breathing roots") erect or knee-shaped: thorny trunks or branches: cauliflory: peculiarities of bark: succulent leaves or stems.

(13) Any special life forms present, e.g. palms or cyads, tree ferns, bamboos, rattans, pandanus.

(14) Trees generally evergreen or deciduous: if mixed, percentages of each form.

(15) If deciduous the time of foliation and leaf fall.

(16) Leaves simple or compound: if compound, pinnate or digitate: approximate number of leaflets.
(17) Leaf size: assignment to one of Raunkiaer's "leaf-size classes" (Fig. 1).
(18) *Life forms of field and ground layers.* General notes on the types present, their frequency and gregariousness, e.g. abundance of tall herbs, ferns, selaginellas, or mosses.
(19) *Periodicity of field layer*: seasonal dying down of any subordinate layer or important constituents: annual plants, if any.

Reproduction.

(20) Seed production of important trees: amount, kind of seed, mode of dispersal (if any). Relation between number of seedling trees and seed-bearing parents. Ability of tree seedlings to endure shade.
(21) Observations on vegetative propagation of trees and shrubs.

Floristic composition.

(22) List of all species distinguished, whether their proper names are known or not; *each layer of the forest should be listed separately.* Where there is a number of species present which the observer is unable to separate and identify by name or number the fact should be noted.

HABITAT

Climate.

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(28) Any corresponding data obtained from the forest itself or its immediate neighbourhood.
(29) Prevailing winds and periodic or seasonal winds of special significance.

Soil and subsoil.

(30) Kind or kinds of rock.
(31) Kind of soil (e.g. sand, gravel, loam, clay, etc.): humus.
(32) Surface litter: nature, depth, rate of disappearance.
(33) Soil profile, with measurements of horizons distinguishable: colour, texture: rooting depths. If there is opportunity for mechanical and chemical analysis, samples should be collected for this purpose, with depths carefully recorded.
(34) Soil-water relations: erosion, run off, depth of water table and its variations at different seasons.

History of the area.

(35) Has the area now occupied by forest ever been cultivated? Any available details about the nature of such cultivation and time of abandonment.

Biotic factors.

(36) Tree felling.
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NOTICES OF VEGETATION

Jepson, W. L. *A Flora of California;* Vol. 3, Part 1, pp. 17–128, figs. 280–365. Berkeley, California, U.S.A. Associated Students Store, 1939. Price, $2·50.

The interest of this book, to ecologists, apart from its use as a means of identifying species, lies in the habitat notes often furnished. These notes are enhanced in value by the intimate and life-long acquaintance of the author with every part of his home State, and his keen powers of observation.

In discussing the woody genus *Arctostaphylos*, of which twenty-five species are described, the author distinguishes between those which possess the capacity to develop regeneration-shoots after the above-ground portion of the shrub is killed by fire or removed by the axe, and those which are completely killed by chaparral fire, and in which the root-crown is not developed into an enlarged structure and has no capacity to send up shoots after fire or after mutilation. The first group he calls "root-crown shrubs"; the second, "fire-type shrubs".

Members of the second type produce seed in abundance, sometimes in astonishing profusion, and promptly repossess burned territory; "they have developed several biological reactions in their life-history, to the circumstances of exclusive reproduction by seed". Root-crown sprouting on the one hand, or fire destruction on the other, are characteristic of certain species; and in this genus reaction to fire appears to provide a species-criterion of value. The occurrence in the same genus of these two kinds of adaptations, which prevent destruction of the species by fire, suggests a possible response to environment. Root-crown sprouting is analogous to the development of hypogeous stems in certain woody plants on the fire-ridden plateaus of Central Africa, as described by the reviewer in *J. Ecol.* **10**, 211–19.

J. Burtt Davy.

A MILESTONE IN PLANT ECOLOGY

Tansley, A. G. *The British Islands and their Vegetation.* Pp. xxxvii+970, 179 text-figures and 416 photographic illustrations. Cambridge University Press. 45s. net.

The publication of this book is an ecological event of the first magnitude, especially perhaps to British ecologists, who have awaited its appearance with interest and who will welcome the comprehensive picture it presents. It is inevitable that comparisons will be made between the present volume and the earlier *Types of British Vegetation*, published 28 years ago and long out of print, and it may be anticipated that this book will prove as useful in stimulating further work as was the earlier one. It is written on broadly similar lines but it possesses a breadth, a unity and detail which were lacking in the older work. Of the nine parts into which the book is divided, the first deals with the physical structure, climate and soils as they affect British vegetation, while the second part deals with the history and present distribution of vegetation. The third part, a short one, deals simply with the elements of the system of classification and terminology employed. All the remaining six parts deal with the details of the vegetation types and the main factors in their relations to their habitats. The accounts are notable not only for the unity which has been achieved in bringing together the results of different investigators but also for the inclusion of much previously unpublished work. From the point of view of its subject matter alone, it seems clear that every student of British vegetation for a good many years will have to refer to this work.

It may be of interest to outline other reasons why the book appears to have considerable significance. In many ways it marks an epoch, the culminating point of a period in which the descriptive study of existing vegetation has been the leading interest of British ecologists. Possibly because there are so many semi-natural types of vegetation in the British Isles, a very large proportion of the ecological work done in this country has been concerned with vegetation and its habitat types, and only to a minor extent have British ecologists been concerned either with autecological studies or with the individual plant-habitat relation. Perhaps as a result neither plant sociology nor the terminology under which plant communities may be arranged has excited much interest in Britain and this outlook is well illustrated in the present pages. This volume, therefore, exactly reflects what has been a main tendency in British ecology and it is fitting that one who has done so much to promote the study of vegetation in Britain, should now be able to bring together a first and comprehensive survey of its main results.

The further comparison of this book with *Types of British Vegetation* will not be without interest because it will reveal notable differences in the outlook on British vegetation as a whole. The most striking of these general differences is undoubtedly the indication that the British Isles contain at least two major climatic vegetation types—*climaxes* in Clement's sense—namely, forest and bog. The former, associated with a series of "deflected successions" is dominant in the south and east, while the latter, except on immature soils, covers the extreme north and west. Between them lies an extensive area which is climatically intermediate and which may perhaps be called a climatic tension zone. In this zone, edaphic or other differences will, no doubt, mainly control the local vegetation types. Further, because much of north-western Britain is mountainous and hence geologically not yet stable, a very great variety of edaphic habitats is presented in the climatic tension zone and there is a corresponding diversity in the types of plant community. For these reasons the British Isles possess an unusual complexity of vegetation types, and this is no doubt the reason for the interest which has been displayed in the analysis and description of vegetation as such, and of communities in relation to their habitat. These reasons may also account for the importance attached to edaphic factors by British ecologists.

The second feature which may be emphasized is that sufficient data are now available for British soils to illustrate the generalization that soils, irrespective of their origin, may tend to assume a steady state in dynamic equilibrium with the climate and vegetation cover. Three clearly distinct climatic types may at present be distinguished in this country, Brown earths, podsols and blanket-bog peats in addition to the topographic types such as fen peats and meadow soils. The treatment of soils along these natural lines has enormously simplified the work of classifying soils for ecological purposes.

At the same time it may be that ecologists have not yet learned how to apply the pedological results to the fullest advantage and it may well be that the soil profile or soil type may prove to be a helpful factor in arriving at a decision on an ecological problem. We are, for example, not quite logical when we recognize *two* extreme climatic vegetation types and *three* climatic soil types. While it is possible that this does represent a correct statement of fact, it may be more probable that in the complexes of vegetation which we include in the term moor (and heath), there lies a nucleus which may represent a distinct climatic grouping coupled with a wide anthropogenic extension in the direction of heath. If this is so the moor (and heath) vegetation type would doubtless then correspond to the podsol type of soil profile when the latter is fully developed.

We then should have an arrangement of the following kind:

Vegetation type	*Soil type*
Deciduous forest	Brown earth
Moor (and heath)	Podsol
Blanket-bog	Deep bog peat

This solution of the problem is partly suggested by the way in which Professor Tansley has arranged the vegetation types of moorland and heath, for while most of the moorland types are included in Part VI, dealing with Hydroseres and hence finally with marsh, fen and bog types of vegetation, heather moors are included in Part VII, Heath and Moor, and the description of heath is preceded by the description of a podsol profile on Cavenham Heath.

Even a brief acquaintance with such soils and their vegetation serves to emphasize the point that their examination in the light of existing conditions is often not enough. It is difficult for a northern ecologist to suppose that the rainfall in East Anglia is at present sufficient to account for the podsolization of some of the Breckland soils, and he would no doubt be tempted to suppose that podsols in that area may have been developed under different conditions of climate or vegetation cover or both, at an earlier date. In the same manner anyone examining the deep cotton-grass peat of the Pennines may well be led to consider whether its formation was initiated under the conditions which exist to-day. The complex of soil, climate and vegetation is, in fact, profoundly affected by the previous history of the site. The third great advance shown in this book is that it is now possible to state for much of the country the general lines of its pre-history and to indicate, at least in a general way, how this has affected the existing vegetation and soil. The inter-relations of our main vegetation types in this country can, in fact, only properly be considered against a background of post-glacial history such as is included in these pages.

It is of interest that this historical method of considering problems of vegetation should serve to focus attention on the biotic factors involved in determining existing vegetation types. The work of Farrow and Watt has shown the importance of these factors at present and the historical method of attack has so emphasized their importance in the past as to suggest that few, if any, British plant vegetation types have been unaffected by the activities of man and grazing animals.

Thus it will be appreciated that one general contribution that this book makes is in summarizing the changed outlook of British plant ecology as it has developed in recent years. There has resulted a striking unification of the fundamental ideas underlying the study of vegetation and possibly this has made a book of this quality feasible. Notable also is it that the Western margins of the British Isles are adequately described for the first time. The fact that all the major British vegetation types are now described in some detail and the more important of their inter-relations indicated, shows that a definite period has been reached in the descriptive ecology of these islands. The thoroughness with which the work has been carried out makes it unlikely that any immediate restatement along similar lines will be profitable. Thus it is permissible to suggest that this book will also initiate a new phase in the study of British vegetation. Certainly it suggests quite definitely certain lines along which further work will progress.

In the first place, it is probable that one result of this work will be an increase in the study of vegetation simply because it will be easier to see what remains to be done and to envisage the problems more clearly. This was the result of *Types of British Vegetation* and there is no reason to doubt that in this case history will repeat itself.

Secondly, it is possible that as our knowledge of vegetation becomes more extensive some simplification or standardization of the methods of describing it will become necessary. It is at times noticeable in this book that the methods of describing plant communities vary very greatly, and it is often the case that the number of species mentioned varies with the individual observer. That this tendency is evident in a book like this where the descriptions have been carefully smoothed out by the author, shows how great must be the real need. It seems certain that what will be required will be some sort of a standard sample plot or series of standard plots adapted to the vegetation types under examination. If these were in common use, a truly comparable series of community descriptions might become available.

Thirdly, there are not wanting signs that greater interest is being taken in observations on plant successions. Although the principle of succession was enunciated and appreciated at an early stage in this country, it is only in very few cases that exact information is available as to the changes of vegetation on a given site. Successions are therefore inferred and not observed. The possibility is pointed out in this book that successions may actually be of a cyclic nature. As an example, the succession from woodland to heath is supposed to be reversible, developing to woodland again and then once more in a natural cycle to heath. That such changes in vegetation may take place is hardly to be doubted by anyone who has watched, for example, the cyclical changes in a lawn or the very striking year to year differences in the composition of a plankton community. But it is clear that the answer to such questions is only to be found in long-term observations of an exact type and many more of such studies are required. Only by the study of changing vegetation and changing habitats can the dynamic problems of ecology be solved.

Lastly, this book also suggests that a new interest is arising in the *structure* of vegetation. Not only are there the problems associated with such features as layering and the arrangement of complementary or stratified communities, but there are also the curious and intriguing questions associated with the number of species in a community. Why should two communities of approximately similar status vary so greatly in structure? The contrast between a *Calluna* moor and a raised bog or between a cotton grass moss and a Connemara blanket bog is very striking at least in the difference in the number of common species, few in the former cases and many in the latter. Similarly it will not escape notice that while some oakwoods contain few species in their ground flora and little but oak in their canopy others have a very mixed canopy and a varied ground flora. In some examples at least, the oakwood with few species is primitive and the presence of numerous species is a sign of disturbance, but it would clearly be dangerous to generalize on these lines although we may perhaps recognize that colonizing communities generally tend to be mixed in composition.

No doubt further elucidation of these points may follow either from further autecological studies or from more detailed analyses of the habitat factors. It may be that a varied or structurally complex plant community implies the existence of a large range of micro-habitats within the given habitat limits and this implies that a real need exists for the analysis of these habitats and the study of micro-habitats in general. Professor Tansley also suggests that much further analysis of climate in relation to plants and to vegetation is required.

No attempt has been made in these paragraphs to indicate other ecological roads which lead away from our present position. They will include no doubt some directed towards various genetic and taxonomic problems, to studies of humus and the soil micro flora, and to the statistical analysis of vegetation. These lie outside the scope of the present work and so need not be considered at this time. Enough has perhaps been said to indicate that this book is not only a mine of information but also a source of inspiration. The illustrations are lavish and of an unusually high quality. It is written in a broad enough manner to appeal to others besides ecological specialists. Hence, quite apart from its ecological significance, this is a notable book and one of great general interest.

W. H. PEARSALL.

LITERATURE ON THE ECOLOGY OF BRYOPHYTES PUBLISHED SINCE 1932

The chapters on Bryocenology and the Ecology of Bryophytes in the *Manual of Bryology* (The Hague, 1932), by Dr H. Gams and the present writer respectively, gave references to the chief literature on these subjects up to their date of publication. The following list includes papers which have appeared since then. General papers with a considerable amount of information about bryophytes are listed, as well as papers dealing specifically with bryophytes. The list does not claim to be exhaustive, especially in the former category. Papers which have appeared in this *Journal* have been omitted.

(1) *Chiefly on bryophyte communities and succession*

Allorge, P. "La végétation muscinale des pinsapares d'Andalousie." *Arch. Mus. Hist. nat. Paris*, 6e sér. **12**, 535–47, 1935. The bryophytes of the *Abies Pinsapo* woods of southern Spain.

Allorge, V. & P. "Sur la présence d'Hépatiques épiphylles aux Îles Açores." *C.R. Acad. Sci., Paris*, **206**, 1323–5, 1938.

Allorge, V. & P. "Sur la répartition et l'écologie des hépatiques épiphylles aux Açores." *Bol. Soc. Brot.* Ser. 2, **13**, 211–31, 1938.

Cain, S. A. & Sharp, A. J. "Bryophytic unions of certain forest types of the Great Smoky Mountains." *Amer. Midl. Nat.* **20**, 249–301, 1938.

Du Rietz, G. E. "Zur Vegetationsökologie der ostschwedischen Kustenfelsen." *Beih. bot. Cbl.* **49**, 61–112, 1932.

Gardet, G. "Notes sur quelques associations muscinales achaliciques du sud de l'Argonne." *Bull. Soc. Bot. Fr.*, **82**, 34–9, 1935.

Grabherr, W. "Die Dynamik der Brandflachenvegetation auf Kalk- und Dolomitböden des Karwendels." *Beih. bot. Cbl.* **55** B, 1–94, 1936. Succession after burning in the Karwendel Mts. (Tirol).

Graff, P. W. "Invasion by *Marchantia polymorpha* following forest fires." *Bull. Torrey Bot. Cl.* **63**, 67–74, 1936.

Griggs, R. F. "The colonization of the Katmai ash, a new and inorganic soil." *Amer. J. Bot.* **20**, 92–113, 1933. Pioneer bryophytes on recent volcanic ash in Alaska.

Griggs, R. F. "Hepaticae as pioneers on nitrogen-free volcanic ash." *Ann. bryol.* **8**, 74–9, 1935.

Jaeggli, M. "Muschi arboricoli del Cantone Ticino (Regione del Castagno, 200–1000 m.). Contributo alla briologia Ticinese, VIII." *Rev. bryol.* N.S. **6**, 23–67, 1933.

Jovet, P. "L'Association à *Fissidens crassipes* Wils. au Parc des Buttes-Chaumont (Paris). Notes de bryologie urbaine, I." *Rev. bryol.* N.S. **5**, 74–82, 1932.

Jovet, P. "Muscinées de quelques cimetières parisiens urbains. Notes de bryologie urbaine, II." *Rev. bryol.* N.S. **6**, 175–8, 1933.

Koch, W. "Ueber einige Wassermoos-Gesellschaften der Linth." *Ber. Schweiz. bot. Ges.* **46**, 355–64, 1936. Bryophyte communities of a Swiss river.

Køie, M. "The soil vegetation of the Danish conifer plantations and its ecology." *Mém. Acad. Roy. Sci. Lett. Danemark*, Sér. 9, **7**, 1–86, 1938.

Koppe, F. "Eine Moosgesellschaft des feuchten Sandes." *Ber. dtsch. bot. Ges.* **50**, 502–16, 1932. Association of *Haplomitrium Hookeri* and *Fossombronia incurva* in northern Germany.

Meusel, H. "Neuere Arbeiten über die Verbreitung und Vergesellschaftung niederer Pflanzen." *Hercynia*, **1**, 327–32, 1939.

Müller, K. "Ueber einige bemerkenswerte Moosassoziationen am Feldberg im Schwarzwald." *Ann. bryol.* **11**, 94–105, 1938. Deals with the following bryophyte communities in the Black Forest (Germany): *Scapanietum paludosae* (springs), late snow patches, subalpine community at unusually low altitude, epiphytes on *Acer pseudoplatanus*.

Negoro, K. "Ueber die Bryophytenassoziationen in den mineralogenazidotrophen Gewässern Japans." *Sci. Rep. Tokyo Bunrika Daig.* Sect. B, **3**, 303–13, 1938. Bryophytes of lakes containing free sulphuric acid and a high percentage of salts.

Ochsner, F. "Études sur quelques associations épiphytiques du Languedoc." *Rev. bryol.* N.S. **7**, 74–104, 1934.

Richards, P. W. "Ecological notes on the bryophytes collected by the Oxford Expedition to Sarawak." In Dixon, H. N. "A contribution to the moss flora of Borneo." *J. Linn. Soc.* (*Bot.*), **50**, 57–140, 1935.

Richards, P. W. "The bryophyte communities of a Killarney oakwood." *Ann. bryol.* **11**, 108–30, 1938.

Størmer, P. "Vegetationsstudien auf der Insel Håøya im Oslofiord." *Norske Vid.- Akad. Skr. M.- N. Kl.* **9**, 1938. Bryophyte communities of various woodland types.

Watson, E. V. "The mosses of Barra, Outer Hebrides". *Trans. Bot. Soc. Edinb.* **32**, 516–41, 1939.

Werner, R. G. "Bryologie et phytogéographie." *C.R. Acad. Sci., Paris*, **207**, 351–3, 1938. Bryophytes characterizing Emberger's "*étages*" of Mediterranean vegetation.

Whitehouse, E. "Plant succession on Central Texas granite." *Ecology*, **24**, 391–405, 1933. Succession on bare rock, in crevices, on gravel and in seasonal pools.

Wilson, B. L. "A bryocenological study of some epiphytic mosses of a central Indiana wood." *Butler Univ. Stud.* **3**(**10**), 149–71, 1936.

(2) *Chiefly on autecology, habitat factors, etc.*

Allorge, P. "Observations sur *Tortula desertorum* Broth., mousse aralo-caspienne des plateaux castillans." *Rev. bryol.* N.S. **11**, 110–12, 1938.

Apinis, A. & Diogucs, A. M. "Data on the ecology of bryophytes. I. Acidity of the substrata of hepaticae." *Acta Hort. Bot. Latv.* **8**, 1–19, 1933.

Apinis, A. & Lacis, L. "Data on the ecology of bryophytes. II. Acidity of the substrata of musci." *Acta Hort. Bot. Latv.* **9**/**10**, 1–100, 1936.

Baas Becking, L. G. M. & Nicolai, E. "On the ecology of a *Sphagnum* bog." *Blumea*, **1**, 10–45, 1934.

Billings, W. D. & Drew, W. B. "Bark factors affecting the distribution of corticolous bryophytic communities." *Amer. Midl. Nat.* **20**, 302–30, 1938.

Clapham, P. M. & Oldroyd, M. "A time-table for the life cycles of some of the liverworts in Yorkshire." *Naturalist*, 253–9, 1936.

De Valera, M. "The distribution of mosses in relation to soil acidity." *Naturalist*, 89–91, 1937.

Fischer, J. "Zur Verbreitungsökologie von *Splachnum sphaericum* (L. fil.) Swartz." *Beih. bot. Cbl.* **55** A, 122–44, 1936.

Gams, H. "Die Verbreitung einiger Splachnaceen und der *Oreas Martiana* in den Alpen (Beiträge zur analytischen Behandlung von Moosarealen, IV)." *Ann. bryol.* **5**, 51–68, 1932.

Gams, H. "Beiträge zur Kenntnis der Steppenmoose." *Ann. bryol.* **7**, 37–56, 1934. *Funaria hungarica*, the alpine *Pterygoneurum* spp. and *Stegonia*.

Gams, H. "Zur Verbreitung und Verwandschaft einiger europäischer Marchantiales (Beiträge zur Kenntnis der Steppenmoose, III and IV)." *Ann. bryol.* **11**, 58–67, 1938. *Grimaldia, Neesiella, Tesselina, Riccia Bischoffii* and *R. Gougetiana*.

Geitler, L. "Hochmooralgen an Kalkfelsen." *Arch. Hydrbiol.* **31**, 678–81, 1937. Production of an acid substratum by mosses on calcareous rocks.

Grebentschikova, A. "Die ökologischen Faktoren und das Wachstum der Sphagnum-Moose." (In Russian.) *Trudy Wsesojusn. Inst. Torfa*, **3**, 73–86, 1933. Abstr. *Bot. Zbl. N.F.* **26**, 144, 1935.

Griggs, R. F. "Growth of liverworts from Katmai in nitrogen-free media." *Amer. J. Bot.* **21**, 265–77, 1934.

Györffy, I. "Monographie der Thermalvegetation von Hajduszoboszlo in Ungarn." *Arch. Protistenk.* **76**, 274–337, 1932. Bryophytes of hot springs.

Haring, I. M. "Plant growth under electric light." *Bryologist*, **33**, 89–91, 1931. Bryophytes in caves illuminated by electric light.

Ikenberry, G. J. "The relation of hydrogen-ion concentration to the growth and distribution of mosses." *Amer. J. Bot.* **23**, 271–9, 1936.

Jaag, O. "*Botrydina vulgaris* Breb., eine Lebensgemeinschaft von Moosprotonema und Grünalgen." *Ber. Schweiz. bot. Ges.* **42**, 169–185, 1933.

Juday, C. "The depth distribution of aquatic plants." *Ecology*, **15**, 325, 1934.

Koppe, F. "Beobachtungen über Frostschaden an Moosen." *Ber. dtsch. bot. Ges.* **49**, 35–51, 1931. An important paper not referred to in the *Man. of Bryol.*

Kotilainen, M. J. "Ueber die Methoden der autökologischen Untersuchung der Felsenmoose." *Mem. Soc. Pro. Fauna Fl. Fenn.* **7**, 90–2, 1932.

Maheu, J. & Guérin, H. P. "Influence de la lumière électrique sur la flore cavernicole." *Bull. Soc. Bot. Fr.* **82**, 477–94, 1935.

Müller, K. "Ueber das Vorkommen von Kalkpflanzen im Urgesteingebiet des Schwarzwaldes." *Mitt. bad. Landesver. Naturk. Naturschutz*, **3**, 129–39, 164–76, 1936.

Nichols, G. E. "Notes on Michigan bryophytes. II." *Bryologist*, **36**, 69–78, 1933. *Tortella tortuosa* found growing *under* quartz pebbles where there is usually no plant life on the surface of the ground.

Ochsner, F. "Verdunstungsmessungen an Epiphytenstandorten." *Ber. geobot. Forschungsinst. Rübel, Zürich*, f.d. Jahr 1932, 19–30, 1933.

Ochsner, F. "Oekologische Untersuchungen an Epiphytenstandorten." *Ber. geobot. Forschungsinst. Rubel. Zürich*, f.d. Jahr 1934, 69–80, 1935.

Pia, J. "Die Kalkbildung durch Pflanzen." *Beih. bot. Zbl.* A, **52**, 1–72, 1934. Tufa-forming bryophytes.

Potzger, J. E. "Microclimate, evaporation stress and epiphytic mosses." *Bryologist*, **42**, 53–61, 1939.

Romell, L. G. "Den nordiska blåbärsgranskogens produktion av ris och förna." *Svensk Bot. Tidskr.* **33**, 366–82, 1939. Litter production and annual growth of mosses in Scandinavian spruce woods.

Schade, A. "Die kryptogamische Pflanzenwelt an den Felswänden des Elbsandsteingebirges und ihre Lebensbedingungen." *Fedde Repert. Beih.* 76: *Beitr. z. Syst. u. Pflngeogr.* **11**, 12–32, 1934.

Schade, A. "Nachträge zum Standortsverzeichnis der Lebermoose Sachsens nebst einigen kritischen Bemerkungen." *S.B. Abh. Naturw. Ges. Isis, Dresden* (1935), 18–86, 1936.

Steere, W. C. "*Bryoxiphium norvegicum*, the Sword Moss, as a preglacial and interglacial relic." *Ecologist*, **18**, 346–58, 1937. Distribution of this sp. with special reference to N. America.

Van Oye, P. "On biogene lime deposits." *Chron. Bot.* **4**, 213, 1938. Tufa formation by mosses etc.

Wallner, J. "Ueber die Beteiligung kalkablagernder Pflanzen bei der Bildung südbayerischer Tuffe." *Bibl. Bot.* **110**, 1–30, 1934.

Zastrow, E. "Experimentelle Studien über Anpassung von Wasser- und Sumpfmoosen." *Pflnforsch.* **17**, 1–70, 1934.

(3) *Growth-forms of bryophytes*

Meusel, H. "Wuchsformen und Wuchstypen der europäischen Laubmoose." *Nova Acta Leopold.* N.F. **3**, 123–277, 1935.

(4) *Physiological papers with a bearing on ecology*

Hagerup, O. "Zur Periodizität im Laubwechsel der Moose." *Kgl. Dansk. Vidensk. Selsk., Biol. Med.* **11**, 1–88, 1935.

Lackner, L. "Ueber die Jahresperiodizität in der Entwicklung der Laubmoose." *Planta*, **29**, 534–616, 1939.

Mägdefrau, K. "Untersuchungen über die Wasserversorgung des Gametophyten und Sporophyten der Laubmoose." *Z. Bot.* **29**, 337–75, 1935.

Mägdefrau, K. "Reviews of recent research: 2. Der Wasserhaushalt der Moose." *Ann. bryol.* **10**, 141–50, 1937. A useful summary of recent work on the water relations of bryophytes.

Renner, O. "Zur Kenntnis des Wasserhaushalts javanischer Kleinepiphyten." *Planta*, **18**, 215–87, 1933.

Roberts, E. A. & Haring, I. M. "The water relations of the cell walls of certain mosses as a determining factor in their distribution." *Ann. bryol.* **10**, 97–114, 1937.

Stålfelt, M. G. "Der Gasaustausch der Moose." *Planta*, **27**, 30–60, 1937.

Wiefel, R. "Worauf beruht das Frischwerden der abgestorbenen Moosblättchen?" *Bot. Arch.* **37**, 1–42, 1935.

Wiefel, R. "Ueber den Membranbau der Moose." *Bot. Arch.* **37**, 101–18, 1935.

Williams, K. T. & Thompson, T. G. "Experiments on the effects of Sphagnum on the *p*H of salt solution." *Int. Rev. Hydrobiol.* **33**, 271–5, 1936.

Ziegenspeck, H. "Inwieweit sind die Sphagnen und andere Moose befähigt im Leben ihre Umgebung auf ein bestimmtes *p*H-Optimum einzustellen?" *Bot. Arch.* **38**, 1–15, 1936.

P. W. RICHARDS.

REVIEW

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 8, No. 2, November 1939

This number, 187 pages, contains eight papers, one large special review, eight other reviews and 155 short notices. Population studies of mammals, birds and insects provide most of the original material, census methods being employed to measure habitat differences in density and fluctuations in time.

W. M. M. Chapman draws together the work done by Oxford ornithologists upon the bird population of a sample of agricultural land, and proves that the summer numbers have not varied greatly over a series of years; while this constancy applies in winter only to the hedge-haunting species. Summer density was, on the average, two birds per acre. L. S. V. Venables extends his survey of bird communities to chalk downland, and finds that, in spite of certain differences, the habitat selection of birds follows similar courses on the seres of heathland and chalk grassland. David Lack continues his record of bird habitat selection in older plantations than those previously studied by him. Both Venables and Lack rely on the method of walking counts.

Dennis Chitty describes the third Canadian Arctic Wild Life Enquiry (for the season 1937–8) and analyses reports from a number of stations, covering a period of abundance in rodent and fur supplies in the North. There are four papers about insect populations. J. P. Glasgow records a 19-month investigation of Collembola (springtails) in grassland soil, by means of sample censuses. Besides some technical advances in method, he gives a very complete analysis of densities and fluctuations, and brings out clearly the patchiness of the distribution of individuals in the soil. A. G. Robertson discusses the results of catching Tipulids (craneflies) in a light-trap, over a period of four years, and tabulates the seasons of activity, sex ratios, and relation of numbers caught to meteorological factors, amongst which moonlight is important. Walter Carter uses sample counts and trapping to determine the movements into various habitats of *Thrips tabaci* in Hawaii, where this species carries a serious disease of pine-apples. C. H. N. Jackson's mathematical treatment of the problem of deducing total populations from the recovery of marked samples, is an important contribution to the theory of the Lincoln Index—here illustrated by materials from tsetse-fly populations in East Africa.

J. Richard Carpenter's special review of Russian (mainly Soviet) work on community ecology, for the first time brings into proper perspective the very extensive researches in ecology which have been going on in the U.S.S.R. Appended to the general discussion is a bibliography of 570 titles.

Shorter reviews deal with the *Journal of Ecology*, an American text-book of animal ecology, the biology of birds, the natural history of North Rona, forestry bibliography and abstracting, British butterflies, and an expedition volume on Iceland. The "Notices of Publications on the Animal Ecology of the British Isles" are contributed by thirteen voluntary workers and give a good conspectus of current work in this country.

Charles Elton.

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING IN THE UNIVERSITY DEPARTMENT OF BOTANY, OXFORD

2–4 JANUARY 1940

Soirée in the Department of Botany

ON the evening of Tuesday, 2 January, about sixty members and guests were entertained at a soirée arranged in the Department by Prof. and Mrs Osborn. A long and interesting series of exhibits was displayed illustrating plant and animal ecology being done in Oxford. An exhibit by Dr J. F. Hope-Simpson illustrated the variation in plants from chalk grassland. Forms of *Leontodon hispidus, Plantago lanceolata,* and *Poterium sanguisorba* from different natural habitats were shown to retain their differences in garden culture. Dr and Mrs J. L. Harley gave maps and photographs of the vegetation of a small raised bog at Thornton Mire in the limestone district of Yorkshire. It had a central *Callunetum* surrounded by belts of *Caricetum paniceae* and *Juncetum acutiflori.* Peat profiles recovered by boring showed Phragmites peat and wood peat of fair thickness below the acidic peat. Very extensive mapping and photography was shown by Dr E. W. Jones of the vegetation of Pipley Swamp, Studland Heath. It lies at the head of a valley drowned by marine transgression and shows three zones of *Sphagnetum, Molinietum,* and *Phragmitetum.* Very interesting profiles of the valley deposits indicated the results of the marine invasion, and specimens illustrated the root systems of plants from the different zones. Dr Jones also showed the results of a detailed transect through Bagley Wood, Oxford, in which a range of soil types was reflected in a vegetational zonation, and he also demonstrated an apparatus for photoelectric measurement of light intensity in the field, by means of a photoelectric cell suspended downwards above a standard reflecting surface.

Dr A. R. Clapham showed photographs illustrating a transect across the New Forest valley bog at Matley Stream, a site visited by the Society during the Summer Excursion. Prof. Osborn also showed a long series of photographs illustrating the vegetation types seen by the party on its summer visit to Studland Heath. He also showed specimens of *Isoetes echinospora* from Little Sea, *I. Drummondii* from Australia and *I. hystrix* from Corsica. Mr Day had set out a series of scale drawings of the root systems in plan and elevation of different species of poplar growing in soils with impeded drainage. The most extreme soils were a fen peat and a Weald clay, and these showed a very superficial root development above the water-table, in strong contrast to that in freely drained sandy drift over chalk at Thetford. An intermediate type was on boulder-clay in Northants. Dr A. R. Clapham showed an extensive series of herbarium specimens illustrating the species of jointed rushes on which he worked with Mr Timms, and the ecology of which he later described to the meeting. They included *Juncus articulatus* L., *J. acutiflorus* Ehrh., the hybrid between these two, *J. obtusiflorus* Ehrh., and an undescribed form of uncertain status, called "large 80" from its chromosome number.

During the course of the evening Prof. Osborn gave a short talk, illustrated by his own very attractive lantern slides of the visit of the eighth I.P.E. to Morocco. He alluded to the topography, administration, peoples, soils and vegetation, drawing many parallels with arid southern Australia. He emphasized particularly the semi-arid soils with a heavy travertine limestone in the *B* horizon, and the frequent removal by erosion of the *A* horizon.

The Annual Meeting

The twenty-sixth Annual Meeting of the Society was held in the Department of Botany of the University, Oxford, on the following day, Wednesday, 3 January, at 10 a.m., the President, Prof. A. G. Tansley, occupying the chair.

The minutes of the last Annual Meeting were read and confirmed, and apologies for absence were reported.

Mr Summerhayes made a provisional estimate of the financial position of the Society at the end of the year's work, and said he expected a substantial favourable balance. He drew attention to an increase in sales to non-members of the *Journal of Ecology*. A very loudly applauded vote of thanks was then given to the two Hon. Treasurers for their "subterranean" activities for the Society. It was proposed by Dr Varley and carried *nem. con.* that Messrs William Norman and Son be reappointed auditors to the Society for 1940. It was proposed from the chair and carried unanimously that the Council's recommendation be adopted, to make a grant of £10 to the Freshwater Biological Association, with a warning that circumstances might not allow the Society to repeat the grant. Dr Turrill having explained that it had unfortunately become necessary to give up during 1940 the experiments of the Society successfully carried on by himself and Mr Marsden Jones since 1928, it was agreed to make a further grant of £5 to enable the Transplant Experiments to be closed, and further action was left in the hands of the Council.

The report of the Hon. Secretaries as adopted by the Council was then approved.

Hon. Secretaries' Report for the Year 1939

The twenty-fifth Annual Meeting of the Society was held in the Botanical Department of University College, London, on Saturday, 6 January. On the previous evening a soirée had been given in the department to some eighty members and guests: a series of interesting exhibits had been shown, and Sir Arthur Hill had given a short talk on flower movements.

The Annual Meeting was held on the Saturday, and after the business meeting the President opened an extremely successful discussion on the Reciprocal Relationship of Ecology and Taxonomy, which was continued through the afternoon. The Society is very grateful to Prof. Salisbury and Prof. Hill for their kindness in having given the Society once more the generous hospitality of their department.

Following upon the success which attended the holding of an additional meeting at Easter 1938, a similar additional one-day meeting was held on 4 April in the Metallurgical Lecture Room, Imperial College of Science, South Kensington. Prof. Tansley gave the Presidential address on "British Ecology during the past quarter-century: the Plant Community and the Ecosystem". A series of five papers on diverse ecological topics followed. Our warm thanks are due to Prof. Brown and Mr G. E. Blackman for making possible such an extremely successful meeting.

The Summer Meeting was held in Southampton from Wednesday, 16 August, to Sunday, 20 August. In extremely favourable weather conditions about thirty members and guests made excursions to Studland Heath, to Forestry Commission areas of the New Forest, to shingle spits and salt-marshes at Hurst Castle and Warren Point, and to a group of New Forest valley bogs. On each of three evenings short papers were given on the geology and topography of the district, and the ecology of the areas visited: in addition exhibits had been set out in the Botanical laboratory, and on the last evening Prof. and Mrs Mangham kindly entertained the Society in their home at Nursling. Those who were present look back on the meeting as exceptionally pleasant and instructive, and the Society expresses its sincerest thanks to our Southampton hosts, particularly Prof. Mangham, and to our guides and instructors, notably Mr D. W. Young, who so ably took charge of the New Forest woodland excursion.

In the past year two numbers of vol. 8 of the *Journal of Animal Ecology* have been issued, appearing in May and November, and containing respectively 225 and 188 pages. Twenty-one original papers with 11 plates, in addition to reviews, the Society's notices, and 343 notices of publications on Animal Ecology were issued in them.

Two numbers of the *Journal of Ecology* have been issued since the last Annual Meeting: they appeared in February and August, and contained respectively 261 and 289 pages. Twenty-one original papers were published with 27 plates, as well as notices, reviews, and the obituary of Prof. Carl Schröter.

The Society's transplant experiments at Potterne have continued to give very satisfactory results in the hands of Mr Marsden-Jones and Dr Turrill.

Since the last Annual Meeting the membership of the Society has remained unchanged at 361 members, 16 members having died or resigned, and 16 others having been elected. Of the present membership list 193 members received the *Journal of Ecology* alone, 116 the *Journal of Animal Ecology* alone, 52 both journals, and 1 neither.

The Council has decided that for the present it will continue to organize the meetings and publish the journals of the Society as before the outbreak of war. It hopes that members will also continue, so far as they are able, to support the Society actively despite the difficulties of these times.

The meeting then proceeded to the election of officers as follows:

President: Mr C. DIVER (Prof. TANSLEY retiring).
Vice-Presidents: Dr A. S. WATT (Prof. HARDY retiring) and Dr O. W. RICHARDS.
Hon. Editor of the Journal of Ecology: Prof. W. H. PEARSALL.
Hon. Editor of the Journal of Animal Ecology: Mr C. S. ELTON.
Hon. Secretaries: Dr H. GODWIN and Dr G. C. VARLEY.
Ordinary Members of Council: Prof. A. G. TANSLEY, Mr J. S. L. GILMOUR, Prof. T. G. OSBORN, Mr D. LACK (all for four years), Dr E. S. RUSSELL and Mr F. T. K. PENTELOW (re-elected for one year).
Retiring Council Members: Prof. A. C. HARDY and Dr W. B. TURRILL.

In the absence of the new President and both Vice-Presidents the retiring President was voted into the chair.

The Hon. Secretaries announced that arrangements were in hand to hold a one-day meeting of the Society in London at Easter, and to hold the Summer meeting in the south-west at either Exeter or Plymouth: further arrangements were left to the Council. The business closed with a very hearty vote of thanks to the two Hon. Editors and the two Hon. Secretaries for their unremitting work on the Society's behalf.

At about 11 a.m. the meeting proceeded to a series of short papers. Prof. A. C. Hardy gave an extremely interesting account of the aerial drift of insects across the North Sea. Nets carried by vessels crossing the North Sea caught many live insects, particularly aphids, and by noting the time and place of capture it was possible to get some idea of the part of the land from which they had come. An average insect population of about 137 millions was reckoned for a central area of the North Sea between sea level and 300 ft. The following took part in the discussion: Prof. A. G. Tansley, Dr G. C. Varley, Dr J. Z. Young, Dr C. B. Williams, Dr H. Godwin, Mr J. S. L. Gilmour, Dr H. C. Gilson, Miss M. F. Mare, and Mr D. Chitty.

Dr A. R. Clapham then gave an account of the ecology of jointed rushes in the Oxford district. *Juncus obtusiflorus* (= *subnodulosus*) grows in the valley fens and hillside fens where there is calcareous water and a water-level maintained high throughout the year: *Juncus acutiflorus* (= *sylvaticus*) is abundant but not dense in meadows beside the Thames, where it is flooded in winter but dry in summer, and where grazing is only light. *Juncus articulatus*

(=*lamprocarpus*) and the hybrid between *J. articulatus* and *J. acutiflorus* are abundant in the grazing meadows, where they seem to resist grazing by virtue of the semi-prostrate lower internodes, the rooting and branching from basal nodes, and the vivipary from inflorescences. In the discussion which followed Prof. A. G. Tansley, Dr P. W. Richards, Mr V. S. Summerhayes and Dr J. H. Harley took part.

There then followed an account by Mr T. G. Tutin of Plant Associations in Submerged Habitats. Mr Tutin described how, as an outcome of his work on the Percy Sladen expedition to Lake Titicaca he had come to doubt the validity of the concept of succession of the lake vegetation to the same climax as the vegetation of the surrounding land. He considered the lake to be a distinct climatic region with its own seres leading to a climax of large brittle-stemmed plants, and proposed the term "limnosere" for this succession, as distinct from the term "hydrosere" which he thought should be restricted to "pond" successions. The "thallassiosere" in the sea was equivalent to the limnosere, and both had under-water climaxes. The extremely wide prospect opened by these suggestions was commented on in the discussion by Dr H. Godwin and Prof. W. H. Pearsall.

Dr J. F. Hope-Simpson then gave an account of the results of recently re-examining the areas of chalk-grassland originally described by Tansley and Adamson in 1919–20. Removal of rabbit-grazing from most communities had led to *Festucetum rubrae*, *Brometa* had changed to the same community, and mixed grassland had become *Brachypodietum*. With increased grazing, communities dominated by *Festuca elatior* or *Arrhenatherum* as well as Calluna chalk-heath had changed to *Festucetum ovinae* or *Agrostido-Festucetum*. These and other changes were demonstrated by records of objective sampling, and by pairs of photographs representing identifiable areas at the beginning and end of the period concerned. Dr A. R. Clapham and Prof. A. G. Tansley spoke in the discussion.

The meeting was continued after lunch with Dr W. B. Turrill in the chair. Dr E. W. Jones gave an account of the factors controlling the distribution of beech and spruce in the Black Forest and Vosges Mts. He pointed out that despite the very great similarity between these two mountain regions in topography and geology the spruce is restricted in the Vosges to very small and localized areas, so that the beech there rises to the tree limit instead of the spruce. Dr Jones inclined to the view that the effect of low winter temperatures was to rob the beech of competitive power against spruce in an easterly and continental direction, thus permitting spruce to extend in a way it cannot in the Atlantic climate of the Vosges.

Prof. A. G. Tansley then took the chair for the opening of a discussion on the Application of Ecology to Present Economic Problems. Mr C. S. Elton described the work which the Bureau of Animal Population was doing to control rats, mice, and rabbits, which use up a large amount of human food "at all stages from the farm to the breakfast table, and possibly beyond". He stressed the importance of a knowledge of the structure of populations in this respect, and the importance of encouraging biological surveys. Mr William Davies stressed the enormous importance of grassland productivity in British agriculture, and described the methods and results of an extensive survey of grasslands of England and Wales, based upon estimates of floristic composition. The vast bulk of this grassland, he said, is of very low productivity, although this could be greatly improved by suitable management.

After an interval for tea provided by our Oxford hosts, the discussion was resumed. Dr Mortimer read and expounded a report from Dr Worthington discussing the productivity of fresh water in both natural and artificial ponds. The use of sewage effluent for manuring the waters was mentioned, and special reference was made to the cultivation of carp and eels. Mr Day said that the war would cause a great deal of clear-felling of woodland, and that ecologists could best operate in advising on the problems of the planting which would have to follow, particularly in relation to the cultivation of exotic trees and the innumerable difficulties raised by the relegation of the forester to the lower grade soils, where factors of excess or deficiency in the habitat operate with special severity on the woodlands. Dr J. F. Hope-Simpson then made a series of specific suggestions as to treatment likely to improve the southern chalk grassland. He suggested attempts to recover to good grazing land now under *Bromus erectus* or *Brachypodiun pinnatum*, rabbit control in areas of severe over-grazing, and the trial of *Dactylis glomerata*, *Phleum pratense* and *Trifolium repens* in establishment of cover on bare areas. Seasonal grazing in relation to the moss/forb balance was emphasized.

Prof. T. G. Osborn asked how the members of the Society could utilize their special knowledge, and hoped for collaboration with scientists already engaged on specific war tasks. He stressed the value of autecological studies in the short-term investigations called for by present circumstances. Dr H. Godwin deplored the gap between the Scientific Advisory Council and the working scientists and wished to bring pressure on the Government departments to make use of biological scientists. Mr W. Davies pointed out the necessity on our part of saying exactly what we are able to do. Dr C. B. Williams and Dr Mortimer also spoke. After some discussion Dr Godwin proposed the following resolution, which was seconded by Dr Clapham and carried unanimously: "That this Society, either alone or in co-operation with other scientific bodies, should take steps to urge upon the Government a more active utilization of the services of biological research workers in the present emergency." It was further agreed "That the Council be asked to implement this resolution."

Dr O. W. Richards then raised the question of the publication of material for a biological Flora. Reference was made to the scheme already begun by the Society, but the general feeling was clear that publication of some material should be put in hand at once. Dr Clapham proposed, and Mr Summerhayes seconded, that the council be asked to take action upon this decision, and this was agreed unanimously.

At 10.15 a.m. on the following morning, 4 January, the meeting was resumed with Dr O. W. Richards in the chair. Mr C. B. Goodhart gave an account of the ecology of estuarine amphipods based on work in the neighbourhood of Hurst Castle. He gave a series of distribution maps and verbal descriptions of the habitats of several species of the genera *Melita*, *Corophium* and *Gammarus*. These habitats showed a great range of salinity conditions. There followed an interesting discussion in which Dr O. W. Richards, Dr D. H. Valentine, Dr G. C. Varley, Prof. A. G. Tansley, and Miss F. M. Mare took part.

Prof. A. G. Tansley then took the chair whilst the Vice-president, Dr O. W. Richards, gave a résumé of his quantitative studies on the population of the Cabbage White butterfly at Slough. The problem was defined as that of estimating numbers with a known degree of accuracy, and it was shown how it was possible to interpret the census data so as to arrive at estimates of the proportion of insects destroyed by various agencies such as predators, birds, disease and climate. Prof. A. G. Tansley, Dr G. C. Varley, Dr G. D. Hale Carpenter, Dr E. W. Jones, Dr H. C. Gilson, Mr G. E. Blackman, and Dr J. F. Hope-Simpson took part in the discussion afterwards.

Dr Richards then resumed the chair, and called on Dr D. H. Valentine for his paper on the distribution of the Primrose and Oxlip in the woods of eastern England. Dr Valentine described the examination of a wood with a central pure oxlip population surrounded by primroses, with an intermediate belt of hybrids. Hybrids were rare in the primrose areas, but abundant in the oxlip area. The explanation was shown to depend on the fact established esperimentally by the speaker, that the cross with the primrose as female parent yields no viable seed, whereas the cross with oxlip as the female parent produces a fair proportion of hybrid offspring. Thus the primrose is invading the oxlip population by its pollen, and will tend to replace oxlip. In the interesting discussion raised by this account the following members spoke: Dr C. B. Williams, Dr G. C. Varley, Mr G. E. Blackman, Dr W. B. Turrill, Prof. A. G. Tansley, Dr O. W. Richards, Dr A. R. Clapham and Dr J. S. L. Gilmour.

Mr H. G. Veevers then gave an account of the different methods which have been used to count gannet populations in the twenty-two colonies known in the world. The work done in conjunction with Mr James Fisher in the 1939 census showed the total population of the species to be about 170,000. Accounts of the history of individual colonies were employed to illustrate the nature of the factors now operating to determine the size and position of gannet populations. Dr O. W. Richards, Dr C. B. Williams and Mr J. S. L. Gilmour asked questions at the end of the paper.

Dr J. L. Harley then described the results of his studies on woodland soils under beech forest in the Chilterns. He compared the three major soil types: Escarpment, *A* type Plateau, and *C* type Plateau in respect of total nitrogen and carbon, carbon dioxide emission, soluble carbon, fungal and bacterial content, rate of mobilization of nitrogen, and available calcium. In all these respects there is the same relation of the three soil types, highest values being in the escarpment soils, and falling off to the Plateau *C* soils. The low density of roots in the surface soil of Plateau *A* type was due to the absence of the restricting factors present in the other soils, shallowness in the one and biological poverty in the other. Heavy mycorrhizal infection was shown to be restricted to the two Plateau soils. Dr Mortimer, Mr Day, and Mr G. E. Blackman raised questions afterwards.

Dr V. J. Chapman then gave an account of the relation of plants to the West Indian shoreline. By lantern slides and specimens he illustrated the beaches and dunes made of "Halimeda sand" with their vegetation. The mangrove vegetation of the shore he related to three soil types, reef, mud, and a fibrous "marine peat" formed slowly in the absence of silting. The low tidal range prevents any pronounced zonation with rising shore-level. Dr E. W. Jones and Prof. T. G. Osborn spoke in the discussion afterwards.

At the close of the meeting Dr O. W. Richards thanked Prof. and Mrs Osborn very heartily for all the trouble they had given themselves to make the meeting so enjoyable, and Dr Godwin expressed a similar gratitude of the Society to Dr Clapham who had borne the burden of the local arrangements, and to the cheerful and efficient laboratory staff.

SUMMER MEETING AT SOUTHAMPTON

16–20 August 1939

Following the kind invitation of Prof. Mangham the Summer Meeting of the Society was held in Southampton, and the opening was held in the Department of Botany at 8.45 p.m. on the evening of 16 August. Prof. W. Rae Sherrifs very kindly gave the Society an illustrated account of the geology and topography of the country round Southampton, and at the end of the evening Mr Diver outlined the programme for the excursion on the morrow.

Thursday, 17 *August*. Under the competent leadership of Mr C. Diver and Dr E. W. Jones the party visited Studland Heath. They were there shown the extensive dune system of known age overlying Bagshot Sand. These dunes differ from most coastal dunes in the extremely low initial content of lime, which seems to be responsible for the absence of all intermediate seral stages between *Ammophiletum* and Calluna heath, as well as the very scanty population of freshwater snails, and the virtual absence of larks and meadow-pipits. Larks are present on the Bagshot beds nearby. The party was shown many interesting developmental stages both of the dunes themselves and of the wet hollows between them. Captain Diver told us about the distribution of grasshoppers in the area, and these insects and their allies got more attention from the zoologists than any other group of animals, because the group is so well represented in these parts by species which are normally regarded as rare. Various members collaborated in the study of grasshoppers, and became expert in their detection by sound alone. It may be worth mentioning that a number of specimens of the rare wasp *Odymerus basilis* Sm. were seen, apparently burrowing in the sand. The party had lunch by the shores of Little Sea, and the magnificent weather encouraged almost all the party to enter the lake, ostensibly to make leisurely investigation of the bottom flora with its carpet of *Isoetes echinospora*. The party then went on to examine the vegetation of Pipley Swamp at the southern end of Little Sea. We were then shown Brand's Bog, a very interesting example of a valley bog, showing a well-marked pool and hummock structure, and a rich Sphagnum flora including *S. auriculatum* var. *sanguinale*, *S. papillosum*, *S. tenellum*, *S. compactum*, *S. pulchrum* and *S. cuspidatum*. *Erica ciliaris* was present on the hummocks. The lower slopes of this bog showed an unusual transition to salt marsh vegetation, through a bog vegetation mixed with *Schoenus nigricans*, then a belt dominated by *Schoenus*, and finally *Juncetum maritimae*.

After tea at the ferry the party drove back to Southampton, and in the evening attended a meeting in the Department of Botany. Mr T. N. Retford gave an account of the Hydrography of Poole Harbour, carried out by the University Department of Geography. The 15 square miles of the harbour is a drowned valley, and has a tidal range of only 2 to 6 ft. Mr Retford discussed the problems of silt movement in the harbour, and suggested that it had no direct marine origin. The role of *Spartina Townsendii* in mud fixation was stressed, the rhizomes of this plant growing at 6 to 18 in. above mean sea-level. It appeared that where channels were now being filled the material was coming from the erosion of unprotected mud flats at low water. Considerable general discussion followed the paper, and then Miss K. Boswell gave an account of the topographical changes in the developing shingle spit system at Warren Point. A series of maps of different dates established that practically all its growth had been made since 1907.

Friday, 18 *August*. The party assembled at Denny Wood on the Beaulieu Road, and Mr D. W. Young explained some of the major ecological features of the New Forest woodlands. There probably had always been heath on the Plateau Gravels and forest on the clays and better soils, with a spiny shrub zone between the two. The absence of coppice shrubs was due to grazing beneath the trees. Pines, introduced in 1783, were now invading the heaths rapidly, and reduction in the herds of deer since 1850 had caused much extension of the holly, especially in the marginal land. The part first examined of the Denny Enclosure was on Barton Sands, and the soil profile was exposed in deep pits which showed only a very slight tendency of the soil to podsolization. These inspection pits in the Forest proved to be very efficient traps for ground beetles, and there was some competition to be first down the hole to discover what had been caught. The party walked to an area above the Headon Beds, where the soil is less satisfactory, bearing *Leucobryum* and *Polytrichum formosum*, with no *Euphorbia amygdaloides* and no regeneration of ash. The soil profile here had a narrow *B* layer with humus and iron pan over gravel. At Vinney Ridge the party saw planted exotic species of many kinds with good natural regeneration. At Knightwood there was 15 in. of peat over Barton Sands with some clay: the accumulation in the *B* layer was irregular and there was strong gleying. This had been planted with Scots pine which was not, however, regenerating. The Bolderswood enclosure on Plateau gravel over Barton Clay carried *Pseudostuga Douglasii*, *Sequoia sempervirens* and Sitka spruce up to 120 ft. high after only seventy years' growth, with a great many fine specimens of other exotic conifers. The party returned to Southampton after tea at Lyndhurst.

In the evening, in the Department of Botany, Prof. Mangham gave an outline of what the excursion might expect to see on the following day. He paid special attention to the progress of *Spartina Townsendii* on this coast, and the growth of the shingle spits. Dr H. Godwin followed with an account of the submerged peat beds revealed in the excavations for the King George V Graving Dock at Southampton. Pollen analyses showed that the beds had begun in the Pre-Boreal period and had continued until marine transgression had intervened not earlier than middle or late Atlantic times. Possible links with the work on Poole Harbour and with Dr Jones's borings in Pipley Swamp were suggested.

Saturday, 19 *August*. The party visited Warren Point, at the end of the Beaulieu River, where Miss Boswell demonstrated the movements of the shingle spits and mud banks. The older ridges supported *Cirsium tenuiflorus*. In a depression behind the shingle ridges was shallow water, said to be fresh enough for cattle to drink. Here was a dense stand of mixed *Scirpus maritimus* and *S. tabernaemontani*. Cutting for hay-rick thatching was in progress, and this was said to favour the former species against the latter. We went on from here to Hurst Castle shingle spit. Here the method of detecting grasshoppers by sound, learned on the South Haven excursion, revealed in the marshes a colony of the grasshopper *Metrioptera roeseli*. Apparently the species had not previously been found on the South coast, the nearest station being the north Kent coast.

In the evening Prof. and Mrs Mangham entertained members to coffee at their riverside home at Nursling.

Sunday, 20 *August*. Under the direction of Dr A. R. Clapham and Dr H. Godwin the party was taken over three representative valley bogs of the New Forest. The first was at Matley Bog, where the flood plain of the central stream has a shallow, silty, basic peat, and bears tall alder wood "carr", very like that in the East Anglian fens. By a series of transitional zones on either flank this passes into the tussocky *Sphagnetum* maintained by drainage flushes from the hillside. In the "splash zone" outside the fen wood there was abundant *Ludwiga palustris*. The region next seen was part of the broad outflow channel of Denny Bog, on the south side of Beaulieu Road Station. The extensive floating vegetation mat over shallow water, and the thin central line of fen wood were very striking. The last of these sites was at Crane's Moor, north of Burley. Here the influence of the hillside drainage was very great, and a series of terraces showed most interesting pool and hummock structure. In the bottom of the valley, relict Phragmites piercing the *Sphagneta* indicated the former deep channel of the stream, and eutrophic influences were more widely indicated by the prevalence of *Schoenus nigricans*.

These New Forest bogs include the rare localities for the large grasshopper *Mecostethus grossus*, several specimens of which were captured.

A communal farewell took place on the Ringwood Road about 3 p.m., and the President expressed the gratitude of all the party to Prof. Mangham and to the organizers and guides who had made this Summer Excursion one of the most pleasurable in the history of the Society.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1939

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears, and *less* Payments in advance:						
Members taking *Journal of Ecology* only	228	17	3			
Members taking *Journal of Animal Ecology* only ...	135	19	6			
Members taking both Journals	118	11	0			
Associates		15	0			
				484	2	9
Interest on Investments	46	15	0			
Interest on Deposit Account		10	6			
				47	5	6
Index volume to *Journal of Ecology*, vols. I–XX:						
Sales	8	4	0			
Expenses	1	5	6			
				6	18	6
				£538	6	9
Journal of Ecology, 1939:						
Sales. Current vol. **27**, 1939	583	10	6			
Back volumes and parts	37	10	5			
Reprints of papers	53	17	6			
				674	18	5
Advertisement					10	0
Grant: From Crown Agents for the Colonies ...				30	0	0
				705	8	5
Balance (see above, under Expenditure)				147	19	3
				£853	7	8
Journal of Animal Ecology, 1939:						
Sales: Current vol. **8**, 1939	271	18	4			
Back volumes and parts	37	0	9			
Reprints of papers	117	15	6			
				426	14	7
Balance (see above, under Expenditure)				201	3	9
				£627	18	4

Expenditure

	£	s.	d.	£	s.	d.
Working Expenses:						
Printing, Stationery, etc.	13	7	0			
Postages and Travelling	10	18	8			
Bank Charges		13	4			
Soirée Expenses	1	16	7			
Audit	4	4	0			
Clerical assistance	15	0	0			
				45	19	7
Nomenclature of Tropical Forest Communities. Typing Report				4	17	2
Grants:						
Fresh Water Biological Association	20	0	0			
Transplants Experiments Fund	5	0	0			
				25	0	0
Journal of Ecology. Cost *less* Sales				147	19	3
Journal of Animal Ecology. Cost *less* Sales				201	3	9
				424	19	9
Balance: Surplus for the Year, carried forward ...				113	7	0
				£538	6	9
Journal of Ecology, 1939:						
Cost: Paper, Blocks, Printing and Binding				721	19	4
Publishers' Commission				86	3	1
Carriage and Postages				37	1	2
Insurance and Sundry Expenses				8	4	1
				£853	7	8
Journal of Animal Ecology, 1939:						
Cost: Paper, Blocks, Printing and Binding				550	9	6
Publishers' Commission				47	19	11
Carriage and Postages				21	9	3
Insurance and Advertising				7	19	8
				£627	18	4

BALANCE SHEET AT 31 DECEMBER 1939

Assets

	£	s.	d.	£	s.	d.
Cash at Bank				208	2	2
Journal of Animal Ecology:						
Balance of Publishing Account for 1939, due from Cambridge University Press				138	0	1
Investments at Cost:						
Brought forward, 31 December 1938	1,072	0	10			
Purchased in March, 1939: £200 of 3½% War Loan	196	16	0			
				1,268	16	10
				£1,614	19	1

Notes *re* Investments:

Totals held, 31 December 1939:	£	s.	d.
£1,050 of 3½% War Loan at cost ...	1,070	6	10
£200 of 5% Conversion Loan ...	198	10	0
	£1,268	16	10

The market value of the above Investments at 31 December 1939:

	£	s.	d.
3½% War Loan at 93½	981	15	0
5% Conversion Loan 108¾	217	10	0
	£1,199	5	0

A further Asset, not valued above, is the unsold Stock of Journals and Index Volumes held by the Publishers for the Society.

(Signed) V. S. SUMMERHAYES.
ALEX. S. WATT.
Hon. Treasurers.

Liabilities

	£	s.	d.	£	s.	d.
Members' subscriptions, prepaid for 1940/41.				8	10	0
Library Fund				1	5	0
Journal of Animal Ecology, vol. **8**, No. 2						
Balance of Printing Account due				211	18	4
General Revenue Account. Surplus in hand:						
Balance at 31 December 1938	1,279	18	9			
Surplus for Year 1939	113	7	0			
				1,393	5	9
				£1,614	19	1

Audited and found correct and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

(Signed) WM NORMAN & SONS,
Chartered Accountants.

120, BISHOPSGATE, LONDON, E.C. 2.

25 *January* 1940

LIST OF MEMBERS (22 JANUARY 1940)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
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E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
E. **Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dhanna College, Lahore, India.
E. **Andersonian Naturalists' Society** (cf. Glasgow).
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E **Bacon**, Mrs Alice; The Technical College, Brighton.
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E. **Bates**, G. H., B.Sc.; The Farm Institute, Penkridge, Stafford.
E. **Bayer**, Dr A. W.; Dept. of Botany, Natal University College, Pietermaritzburg, S.A.
E. **Bell**, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
A. **Bertram**, Dr G. C. L.; St John's College, Cambridge.
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II. THE DEVELOPMENT OF VEGETATION IN RELATION TO NITROGEN SUPPLY AND SOIL MICRO-ORGANISMS ON JAN MAYEN ISLAND

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(*With three Figures in the Text*)

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INTRODUCTION

THE general programme of botanical work undertaken on the Imperial College of Science Expedition to Jan Mayen was outlined in the first paper of this series (7). This also contained an account of the main characteristics of the vegetation, and the floral composition of the various communities. The environmental factors responsible for the differentiation of the various types of vegetation were indicated but no detailed discussion as to the relative importance of individual factors was attempted. The influence of nitrogen supply in determining the distribution of the vegetation is considered in the present paper.

Although in temperate regions it is well established that nitrogen level is a factor of great ecological importance, singularly little is known concerning the supply of nitrogen in arctic regions and its effect on plant growth. On general grounds it would be expected that the levels of both total and available nitrogen would be low, except in areas close to the nesting grounds of birds and the lairs of foxes and other mammals. Inorganic nitrogen in the soil is derived mainly from the decomposition of organic matter and from fixation by bacteria, while small amounts are contained in rain. Vegetation is in general sparse in the arctic and the amount of nitrogen derived from dead tissue is accordingly small; moreover, the low soil temperatures should restrict the activity of the micro-organisms responsible for the decomposition of organic matter and the fixation of atmospheric nitrogen. Furthermore, legumes are usually absent in arctic regions.

It is difficult to estimate the extent to which leaching occurs but probably it is considerable, not only on account of the porous nature of the ground which results from the small development of soil, but also because of the sudden release of water in large quantity when the snow melts in spring. Descriptive ecology lends support to the supposition that nitrogen supply exerts an important effect on the development of arctic plant communities, for the most luxuriant vegetation occurs almost invariably in the neighbourhood of bird cliffs. It is not suggested that this effect is necessarily due solely to increased nitrogen. Other nutrients, especially phosphorus, will also be increased and are no doubt responsible in part for the greater growth.

In order to demonstrate the importance of the nitrogen effect in any locality, a quantitative investigation is clearly necessary. Accordingly the soil survey reported in this paper was planned before leaving. The proper equipment for the determination of inorganic nitrogen in the soil was taken on the expedition, since it is essential to carry out these observations *in situ* and not on stored samples. These estimations as well as determination of *p*H were carried out by Mr Alexander King, the leader of the expedition. Replicated samples were brought back to England for further study. Mr D. Ward Culter of Rothamsted Experimental Station has since investigated the Protozoa, while Dr S. E. Jacobs has studied the bacteria at the Imperial College. Total nitrogen and total organic matter have been determined by Mr A. G. Pollard. Further analytical work, now in progress, will be reported later. It must be emphasized that the investigation could not have been undertaken without the generous co-operation and advice of these workers.

ANALYTICAL METHODS

Inorganic nitrogen. For these analyses, which were carried out at the Expedition Base on Jan Mayen, it was not possible to use any elaborate apparatus; colorimetric methods, dependent on the Lovibond Nessleriser and the appropriate standards, were consequently employed. Soil extracts were prepared in distilled water to which 10% sodium chloride had been added and were cleared with barium sulphate (Kahlbaum); after filtering, the extracts were perfectly clear. Nitrate was determined by the method of Blom & Treschow (**3**), while for nitrite the Griess-Ilosva method was employed. For the estimation of ammonia aliquots of the soil extracts were distilled after the addition of magnesium oxide, the distillate containing the ammonia was collected in an efficiently cooled receiver, and analysed by the standard Nessler method. It may be mentioned that the Bennett balance (as supplied by Messrs Baird and Tatlock) proved a most suitable instrument for weighing out the soil samples.

Total nitrogen was determined by the Kjeldahl method, while the *loss by ignition* figures were obtained by heating oven-dried material in a muffle furnace at 800–1000° C.

Bacteriological examination. The samples were examined for the presence of *Azotobacter*, nitrifying and cellulose-reducing bacteria as well as sulphate-reducing organisms; the culture work being carried out at 20° C. In the test for *Azotobacter*, sterile mannitol solutions were added to the soils, and after 10 days' incubation the soils were plated out on nitrogen-free mannitol agar. The resulting *Azotobacter*-like growths were replated after 3 days' incubation and, after further purification, the presence of *Azotobacter* was confirmed by microscopical examination. For the other groups of bacteria samples of soil were inoculated into the following media: Winogradsky's ammonium sulphate solution for nitrifiers, Dubos' medium for cellulose-reducing bacteria and Van Delden's asparagin-lactate medium for the sulphate-reducing organisms. The cultures of nitrifying bacteria were tested for nitrite after 4 weeks' incubation, while the other cultures were examined from time to time over a period of 12 weeks. Subcultures were made when positive reactions occurred. These were successful, except in some cases of the cellulose bacteria. Whenever possible an estimate of the activity of the bacteria in the soil was made on the basis either of the rapidity with which the desired reaction appeared in the cultures, or the intensity of the reaction after a fixed time.

CLASSIFICATION OF THE SOIL SAMPLES IN RELATION TO THE PLANT COMMUNITIES

Soil samples were collected from numerous localities on the island, and for convenience in presentation they have been classified into three categories: (i) the main series of twenty-one samples from typical areas of the principal plant communities, (ii) a series of samples from a single slope beneath a bird cliff in the Fishburn Valley, (iii) samples from special localities.

The samples have been grouped according to the type of vegetation growing in the areas sampled. It must be emphasized that the grouping is based entirely on ecological observation; unfortunately, it was impracticable to make any quantitative measurement of the vegetation. As the various conclusions to be advanced in this paper depend upon observed differences in the vegetation, a résumé of the different communities will be made here. For further information the ecological description of Jan Mayen already published in this *Journal* (**7**) may be consulted, and the appropriate reference numbers to the ecological description are given in Tables 1–3.

Series I. Principal plant communities

These samples have been classified into five groups based on the increasing luxuriance of the vegetation, a classification which is necessarily somewhat arbitrary. The first three groups show progressive stages of increasing plant density up to the densest vegetation in localities which did not receive animal droppings. The last two groups are from localities where this factor was of importance.

Group A. Vegetation absent or sparse. The three samples in this group represent the most barren localities studied. Nos. I and II were from the "Volcanic Desert" at Jameson Bay. This interesting region originated from a dust eruption only a little more than 100 years ago. The desert consists of level stretches of fine ash between small cinder cones ((7), p. 164 and Pl. 11). The level area from which sample I was taken was barren of vegetation while the soil was not yet fully consolidated; sample II, on the other hand, was from one of the cones where a very sparse vegetation occurred. Sample III was made on a scree slope near the northern coast where very occasional small plants occurred.

Group B. Vegetation open. Mosses dominant. Vascular plants infrequent. Under this heading are included the localities most typical of Jan Mayen. Mosses (mainly *Rhacomitrium* spp.) were dominant, though a number of vascular plants occurred, usually as rather stunted individuals. Vegetation of this general type covered both the majority of exposed hillsides ((7), p. 162 and Pl. 10) and some of the older lava fields. Sample IV was taken from a lava field, while nos. V–VII are from typical hillside localities. Sample VIII was collected from a stabilized moraine slope on which the vascular plants were more important than in the other localities in this group. Here *Salix herbacea* was frequently the dominant plant, while such species as *Empetrum hermaphroditum* also occurred.

Group C. Vegetation closed: vascular plants dominant. Sample IX is from a solifluction area on which *Salix herbacea* and *Equisetum arvense* were dominant. Sample X was taken on a hillside which supported a varied vegetation of vascular plants. Samples XI–XIII were made on "Sibbaldia" banks ((7), p. 166) which bore the most luxuriant vegetation on the island excluding only those localities enriched by bird and animal droppings; *Sibbaldia procumbens* and *Taraxacum croceum* constituted a major part of the vegetation and a number of other species were confined to these localities. Sample XI was from a less luxuriant bank than samples XII and XIII.

Group D. Vegetation open: controlled by biotic factors. The localities frequented by birds and mammals have been divided into two floristic groups. In the present group are samples from regions where the incidence of droppings was comparatively low. Samples XIV and XV were from below a bird cliff bordering on the volcanic desert. Sample XVI was from the same slope at

Cape Trail as sample XX, but was considerably farther from the cliff face; here the vegetation was only slightly more luxuriant than that of localities where birds did not congregate.

Group E. Vegetation closed: controlled by biotic factors. The five samples considered were from situations in which the maximum effect of animal excreta was shown. Sample XVII was taken from a ledge on the face of a bird cliff where there was a dense vegetation of *Cochlearia groenlandica* and *Saxifraga rivularis*. Sample XVIII was collected from the site of a station occupied by an expedition in 1882–3. The locality elsewhere supported a very sparse vegetation, but in the immediate vicinity of the ruined station *Oxyria digyna* formed a closed community. Samples XX and XXI were collected from localities which supported the most luxuriant vegetation found on the island. The former was on a moist slope below a bird cliff where a dense growth of grass (notably *Festuca vivipara*) and other plants occurred. The latter sample was from an arctic fox lair in the neighbourhood of which there was a specialized flora of vigorous growth. *Alchemilla* cf. *glomerulans*, which was not found elsewhere on the island, was dominant; a number of other species rarely found in other communities (*Potentilla alpestris*, *Gnaphalium supinum* and *Veronica alpina*) also occurred.

Series II. "Bird Cliff" communities, Fishburn Bay

This series of samples was taken from a single slope below a bird cliff at Fishburn Bay ((7), p. 173 and Fig. 2). A detailed account of the vegetation of this locality has been published already, and only the salient features will be mentioned. The slope was chosen for special study on account of the marked zonation of the vegetation which evidently resulted, in part at any rate, from the uneven distribution of the bird droppings. The most luxuriant zone was immediately at the foot of the cliff face where the soil received the greatest amount of droppings from birds nesting on the ledges above. Descending the slope the vegetation became progressively less dense and its floristic composition altered. The vegetation was mapped by taking four transects down the slope, and it was thus possible to distinguish five zones of vegetation. Zone I was at the top of the slope where the vegetation was most luxuriant and zone V at the bottom, some 100 yards from the cliff face. The zones and transects from which the samples were taken are shown in Table 2, where a brief résumé of the vegetation in the various zones is given.

It should be mentioned that sample XXIX, which is placed at the bottom of the table, was from the debris of a rock slide. Vegetation was recolonizing this area and was most closely allied in type to that of zone III.

Series III. Special situations

The five samples shown in Table 3 have been reserved for separate consideration on account of the special conditions of the various localities represented, namely, a "late snow" area and a steam blow-hole. The characteristics of these localities will be outlined when the data are presented.

EXPERIMENTAL RESULTS

The nature of the data precludes the possibility of statistical analysis. The estimations of the soil nitrogen were quantitative, but the microbiological observations and the classification of the vegetation were necessarily qualitative. The main findings have been set out in Tables 1–3, and the divisions of the data into these tables corresponds to the three categories of soils described above, namely series I–III. Before discussing the more general conclusions the data for the several headings and the main groups will be considered separately.

Series I. Principal plant communities

On account of the great importance of the micro-organisms of the soil in determining the relative levels of the nitrogen fractions it will be convenient to examine the distribution of bacteria and Protozoa before discussing the detailed analytical results. The various data are given in Table 1.

A. *Bacteria.*

Azotobacter was present in all the samples excepting only sample I. The search for this organism was extremely thorough, but the method employed did not permit any estimate of the relative activity of the bacteria in the different samples; it should also be borne in mind that the presence of *Azotobacter* does not necessarily indicate that it is actively engaged in nitrogen fixation. The absence of *Azotobacter* from sample I and its presence in sample II are of interest. Both samples came from the volcanic desert where the laval ash is of comparatively recent origin. Sample I was taken in an area where vegetation was absent and the ash still partly unconsolidated. Neither bacteria nor Protozoa were found, and there was no measurable quantity of organic nitrogen. Sample II from a more consolidated situation contained three species of Protozoa and a low concentration of organic nitrogen as well as *Azotobacter*. Moreover, a very sparse vegetation—the first stage in the colonization of the area—was present.

Nitrifying bacteria. There was a very marked correlation between the activity of the nitrifying bacteria and the presence of vegetation. Nitrifying bacteria were absent from the majority of localities where the vegetation was sparse. On the other hand, they were most abundant in localities where there was a luxuriant vegetation associated with the accumulation of bird or mammal excreta. It may be noted that where there was a well-developed vegetation in areas unfrequented by animals (samples XII and XIII) the activity of nitrifying organisms on the basis of the laboratory tests was very low. This indicates that the occurrence of these bacteria is correlated directly with the distribution of animal droppings.

Table 1. *Soil survey on Jan Mayen. The localities are classified in terms of the increasing luxuriance of the vegetation according to the criteria set out on p.* 271

No.	Locality	Vegetation type	Moisture %	*p*H	Inorganic nitrogen (p.p.m.) NO_3	NO_2	NH_3	Total	Total nitrogen %	Loss on ignition %	Bacteria *Azotobacter*	Nitrifying	Protozoa (no. of species) Flagellata	Rhizopoda	Ciliata	Total
				Group A. Vegetation absent or very sparse												
I	Jameson Bay	6	16·88	7·2	Nil	0·072	Nil	0·07	Nil	2·116	0	0	0	0	0	0
II	„	6	17·68	7·2	Nil	0·073	Nil	0·07	0·006	0·062	×	0	2	1	0	3
III	Vogelberg	15	10·02	7·1	Nil	0·017	0·32	0·34	0·013	1·106	×	0	*	*	*	*
				Group B. Vegetation open—mosses dominant—vascular plants infrequent												
IV	West Cross Bay	1	12·42	7·2	Nil	0·017	0·14	0·16	0·015	0·435	×	0	*	*	*	*
V	Neumayerberg	2	15·85	7·2	Nil	0·036	0·23	0·27	0·049	2·333	×	0	4	1	0	5
VI	Wilczec Valley	2	14·80	7·2	Nil	0·176	0·41	0·59	0·053	5·118	×	0	2	3	0	5
VII	Wildberg	2	11·16	7·3	Nil	0·068	Nil	0·07	0·008	1·706	×	×	*	*	*	*
VIII	Fishburn	5	7·00	7·2	0·19	0·026	0·29	0·51	0·019	0·883	*	*	5	3	0	8
				Group C. Vegetation closed—vascular plants dominant												
IX	Fishburn	13	10·02	7·3	0·50	0·013	0·26	0·77	0·070	6·693	×	0	3	1	0	4
X	„	4	21·48	7·1	0·19	0·006	0·13	0·33	0·105	6·010	×	0	3	2	1	6
XI	Wildberg	9	11·92	7·1	0·17	0·014	0·34	0·52	0·119	1·349	×	0	*	*	*	*
XII	Fishburn	9	28·48	7·2	0·91	0·070	0·43	1·41	0·170	7·656	×	×	3	1	0	4
XIII	„	9	44·36	7·2	1·17	0·054	0·47	1·69	0·353	15·787	×	×	4	3	1	8
				Group D. Vegetation open—controlled by biotic factors												
XIV	Jameson Bay	20	9·94	6·0	0·17	0·017	0·30	0·48	0·060	4·279	×	×	6	1	1	8
XV	„	20	13·38	7·1	0·17	0·014	0·28	0·46	0·006	0·417	×	× × ×	4	6	1	11
XVI	Cape Traill	20	11·92	7·2	0·17	0·068	0·40	0·63	0·230	6·680	×	0	*	*	*	*
				Group E. Vegetation closed—controlled by biotic factors												
XVII	Mary Muss Bay	19	12·42	7·2	0·08	0·017	0·40	0·50	0·065	1·603	×	× × ×	*	*	*	*
XVIII	Walrus Gat	20	11·48	7·2	0·51	0·034	1·07	1·61	0·103	2·191	×	× × ×	*	*	*	*
XIX	Austrian Station	22	13·65	7·2	Nil	0·312	0·46	0·77	0·013	0·088	×	× ×	6	6	4	16
XX	Cape Traill	20	57·84	7·2	0·49	0·097	1·92	2·51	0·631	16·832	×	× × ×	7	6	3	16
XXI	Hope Bay	21	32·96	7·1	0·22	0·312	0·30	0·53	0·222	7·656	×	× × ×	*	*	*	*

Notes. The numbers in the column headed "Vegetation type" refer to the types described in Russell & Wellington (7).
Nitrifying bacteria: activity indicated by the number of crosses.
× = presence of species. * = no sample taken.

Sulphate-reducing bacteria. These were found in eleven of the twenty samples of series I which were tested, namely, samples III, V, VI, IX, XI, XII, XIII, XVI, XVIII, XIX, XX. Of the three samples from group A (Table 1) only one gave a positive reaction, two of the four samples from group B were positive and four out of the five in group C. Thus in these groups there was a fairly marked correlation between the sulphate-reducing bacteria and the vegetation. Comparing now groups D and E controlled by biotic factors, it is striking that none of the samples in group D, where the vegetation was open, contained sulphate-reducing bacteria, while four of the five samples in group E gave positive reactions.

Cellulose-decomposing bacteria. Evidence of the presence of aerobic cellulose-decomposing bacteria was obtained in the primary cultures of eleven soils out of the twenty examined, namely, samples III, V, VI, X, XI, XII, XV, XVI, XVIII, XIX, XX. Eight of these fall into the groups where the vegetation was most abundant. Too much reliance must not, however, be placed on these results since not all of the subcultures succeeded. Possibly the abundant fungi, present in many of the primary cultures, overgrew the bacteria.

B. *Protozoa.*

The length of time which elapsed between the collection of the samples and their examination precluded a quantitative estimate of the protozoal population, so that only the number of species present was determined. The distribution of the species between the groups Flagellata, Rhizopoda and Ciliata is shown in Table 1. A close correlation between the number of species, the nitrogen supply and the vegetation is evident. The highest numbers of species were in samples XIX and XX which were characterized by high nitrogen and from areas with an especially luxuriant vegetation. On the other hand, Protozoa were absent from sample I.

Like the nitrifying bacteria, Protozoa show a correlation with animal excreta. This is especially the case with the Ciliata, for the development of which a large bacterial population is necessary. Twenty-four records of ciliates were made and of these all but three were from localities in which there was an accumulation of bird or animal droppings. The Flagellata were the most widely distributed group, *Heteromita globosa* being present in all samples where any protozoa were found while *Oicomonas termo* and *Cercomonas crassicauda* were nearly as widespread. It is hoped that a detailed account of the Protozoa, which number thirty-six species, will be published elsewhere.

C. *Inorganic nitrogen.*

The data in Table 1 shows that the level of inorganic nitrogen in the soil was extremely low. The highest value was 2·51 parts per million in sample XX, while in the majority of localities it did not exceed 1 part per million. The proportions of nitrate-nitrogen and ammonia-nitrogen are by no means constant and are related to the type of vegetation.

Nitrate nitrogen was absent from all but one of the localities bearing an open vegetation. In direct contrast it was present in all areas where the vegetation was well developed, excepting only sample XIX. Even, however, in localities where nitrate was found, the level was extremely low.

Nitrite nitrogen was detected in all the samples but in some cases only in amounts approaching the limits of analytical error. Once again a correlation with the density of vegetation is noticeable, but the presence of nitrite in sample I—a soil which contained no nitrifying bacteria—suggests that small amounts of nitrogen in this form may have had rain as their source.

Ammonia nitrogen was found in remarkably small amounts. The maximum value is 1·92 p.p.m., while in the majority of situations it is less than 0·50 p.p.m. The higher values once again occur in localities frequented by animals. Ammonia was absent in a few of the samples from localities where the vegetation was sparse and the total nitrogen level low.

D. *Total nitrogen.*

The concentration of total nitrogen ranged from nil in sample I to 0·631 % in sample XX. In general total nitrogen content bears the same relationship to the type of vegetation as does inorganic nitrogen, the soils with the highest values are those which bear the densest vegetation. In all cases the inorganic nitrogen is but a small fraction of the total nitrogen present.

Hydrogen-ion concentration.

It will be seen from Table 1 that little variation in *p*H occurs. The values are all within the range 7·1-7·6, with the exception of one sample (XIV) from a "bird cliff" where the value was 6·0.

Series II. "Bird Cliff" communities, Fishburn Bay

The results for the series of soil samples collected from the slope beneath the bird cliff in Fishburn Bay are given in Table 2. The data for the various zones show marked similarity with the corresponding figures for communities of like character in other parts of the island. In the luxuriant closed communities near the cliff face the nitrogen contents were of the same order as those in other localities with a well-developed vegetation (e.g. XII, XIII, XVIII and XX). Likewise, Protozoa species were numerous and nitrifying bacteria showed marked activity. Farther away from the cliff face, where droppings were less frequent, there was a very marked fall in the levels of both total and inorganic nitrogen, while the number of Protozoa and the activity of nitrifying bacteria decreased. Sulphate-reducing bacteria showed a similar distribution, being present only in the more luxuriant zones. The same is partly true of the cellulose-decomposing bacteria which were found in samples XXII, XXIII and XXIV but also in XXVII. Concurrently with the decrease in nitrogen and micro-organisms the vegetation became more open until in zone V there were

Table 2. *Soil survey on slope below Bird Cliff, Fishburn Valley—Jan Mayen*

No.	Zone	Transect	Moisture %	*p*H	Inorganic nitrogen (p.p.m.)				Total nitrogen %	Loss on ignition %	Bacteria		Protozoa (no. of species)			
					NO_3	NO_2	NH_3	Total			*Azotobacter*	Nitrifying	Flagellata	Rhizopoda	Ciliata	Total
XXII	I	B	8·96	7·3	1·390	0·004	0·613	2·007	0·171	0·437	×	× × ×	6	6	3	15
XXIII	I	C	18·28	7·3	1·100	0·007	0·780	1·889	0·319	13·066	×	× ×	4	4	3	11
XXIV	II	D	20·18	7·2	0·188	0·021	1·173	1·382	0·216	6·717	×	×	7	2	2	11
XXV	III	B	6·16	7·3	0·799	0·005	0·469	1·273	0·136	4·014	*	*	*	*	*	*
XXVI	III	D	4·98	7·2	0·389	0·004	0·178	0·581	0·051	2·205	*	*	*	*	*	*
XXVII	IV	B	3·56	7·3	Nil	0·003	Nil	0·003	0·007	0·059	×	0	3	2	1	6
XXVIII	V	C	1·32	7·2	Nil	0·002	0·051	0·053	Nil	Nil	×	×	3	1	0	4
XXIX	†	A	4·98	7·5	0·188	0·021	1·173	1·382	0·144	0·610	×	× × ×	4	2	3	9

Vegetation of the zones:		
	I	Luxuriant closed vegetation dominated by *Oxyria digyna*.
	II	Closed vegetation with *Oxyria*, *Taraxacum croceum* and *grasses*.
	III	Open patches, *moss*, *Salix* and other species.
	IV	Open, rather sandy, *Halianthus* dominant.
	V	Open, occasional *Halianthus*.
	†	A poorly developed vegetation, corresponding to zone III, in a stabilized hollow on a loose rock slide.

* = No sample taken.
Further details are given by Russell and Wellington (7).

Table 3. *Soil survey of Jan Mayen—special situations*

No.	Locality	Vegetation type	Moisture %	*p*H	Inorganic nitrogen (p.p.m.)				Total nitrogen %	Loss on ignition %	Bacteria		Protozoa (no. of species)			
					NO_3	NO_2	NH_3	Total			*Azotobacter*	Nitrifying	Flagellata	Rhizopoda	Ciliata	Total
					(i) Late snow area: Retreat of snow											
XXX	Fishburn	16	24·92	7·3	0·32	0·040	Nil	0·36	0·109	9·094	×	0	3	3	0	6
XXXI			25·58	7·3	0·38	0·040	Nil	0·42	0·108	7·024	×	× ×	*	*	*	*
					Vegetation fully developed											
XXXII	Fishburn	—	26·16	7·6	Nil	0·016	Nil	0·02	0·141	6·703	×	×	3	1	1	5
XXXIII			22·10	7·3	Nil	0·019	Nil	0·02	0·112	7·076	×	× ×	*	*	*	*
					(ii) Steam vent											
XXXIV	Egg Bluff	18	16·78	7·3	0·36	0·048	1·66	2·07	0·006	2·720	×	× × ×	3	0	0	3

Note. The numbers in the column headed "Vegetation type" refer to the types described by Russell & Wellington (7).
* = No sample taken. The activity of the nitrifying bacteria is indicated by the number of crosses.

only occasional plants of *Halianthus peploides*. Thus there seems no doubt that the increase of nitrogen supply by bird droppings is directly related to the density and zonation of the vegetation. Other edaphic factors, among them phosphorus supply and the mechanical nature of the soil, are no doubt subsidiary causes.

Series III. Special localities

(*a*) *Late snow areas.* The data for four samples (nos. XXX–XXXIII) from a late snow area in Fishburn Valley are given in Table 3. Such areas are characterized by the snow lying late into the summer. After the snow retreats plant growth is particularly rapid. Samples XXX and XXXI were taken on 16 August from the edge of the retreating snow. The samples are replicates from situations about 20 m. apart. Samples XXXII and XXXIII were made some 10 m. distant from the snow edge. Here the soil had been uncovered for about 3 weeks and the vegetation, mainly *Oxyria digyna* and *Cerastium cerastioides*, was already so far advanced that many plants were in flower. The replicates in each case show good agreement, and a comparison of the two sets indicates that, associated with plant development, there was a complete removal of nitrate nitrogen. No ammonia was present in any of the samples although the total nitrogen values were comparable with those for localities where a significant ammonia content was found. *Azotobacter* was present in all four samples while nitrifiers were present except in sample XXX. Sulphate-reducing bacteria were absent only from sample XXXIII, and cellulose-decomposing bacteria were found in all samples except XXXII. Several species of Protozoa were also present.

(*b*) *Steam vent.* Sample XXIV was taken at the mouth of a small steam vent on Egg Bluff which is, at the present day, almost the only evidence of volcanic activity on the island. The substrate was similar to that of the "volcanic desert" (cf. sample I). Unfortunately, the temperature was not measured, but it was considerably above that of the surrounding area. At the edge of the vent there was a meagre development of the moss *Bryum argenteum*, although the neighbouring slopes were entirely without vegetation. Compared with the majority of other localities the level of inorganic nitrogen was high, the greater part of it being in the form of ammonia. Total nitrogen was low, while all the bacteria tested for were present though only three species of Protozoa occurred.

DISCUSSION

In order to bring out the broad differences between the various soil samples the major part of the data has been summarized graphically in Figs. 1, 2, 3 which correspond to Tables 1, 2 and 3 respectively. Both from Fig. 1 for the general series and Fig. 2 for the Fishburn bird cliff area it is evident that the density of vegetation is closely correlated with the supply of nitrogen, especi-

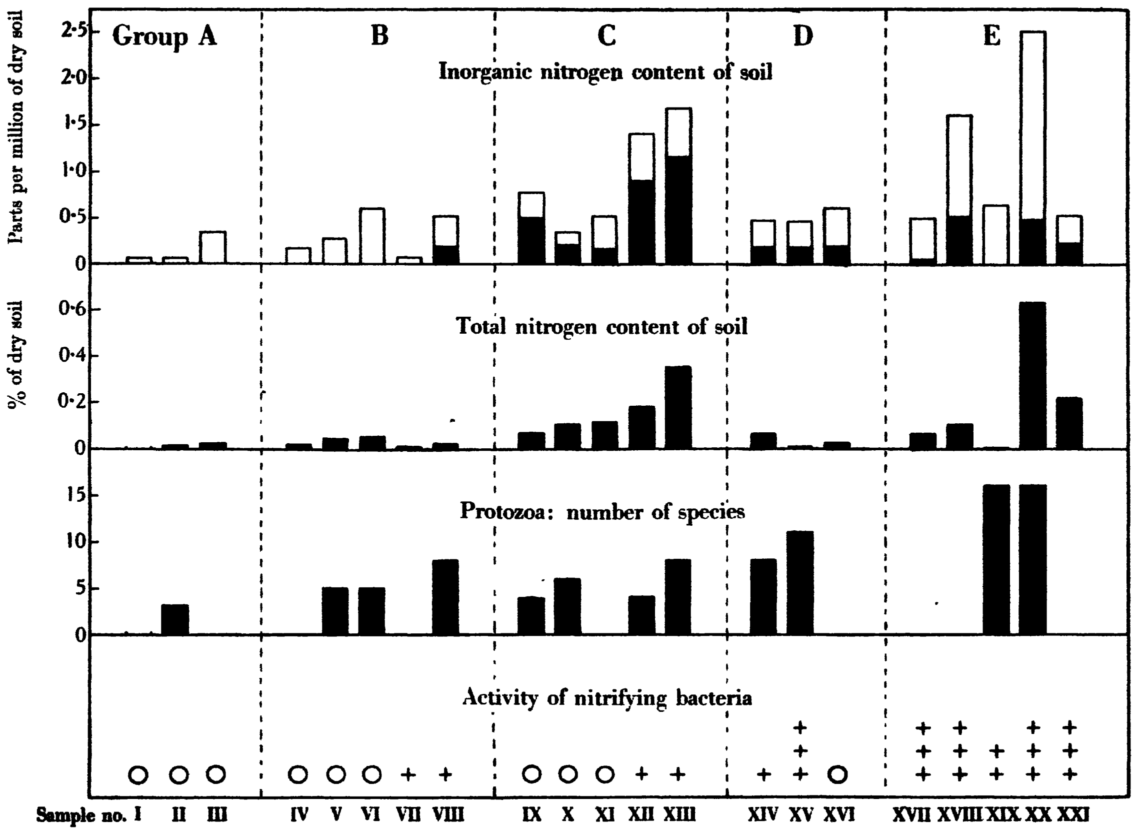

Fig. 1. Data for soil samples from series I. Total nitrogen expressed as percentage of oven dry soil, inorganic nitrogen as parts per million. The nitrate-nitrogen fractions are represented by the unshaded portions of the histograms. Except for a few samples when no examinations were made, the number of protozoa species and the activity of the nitrifying bacteria are also given.

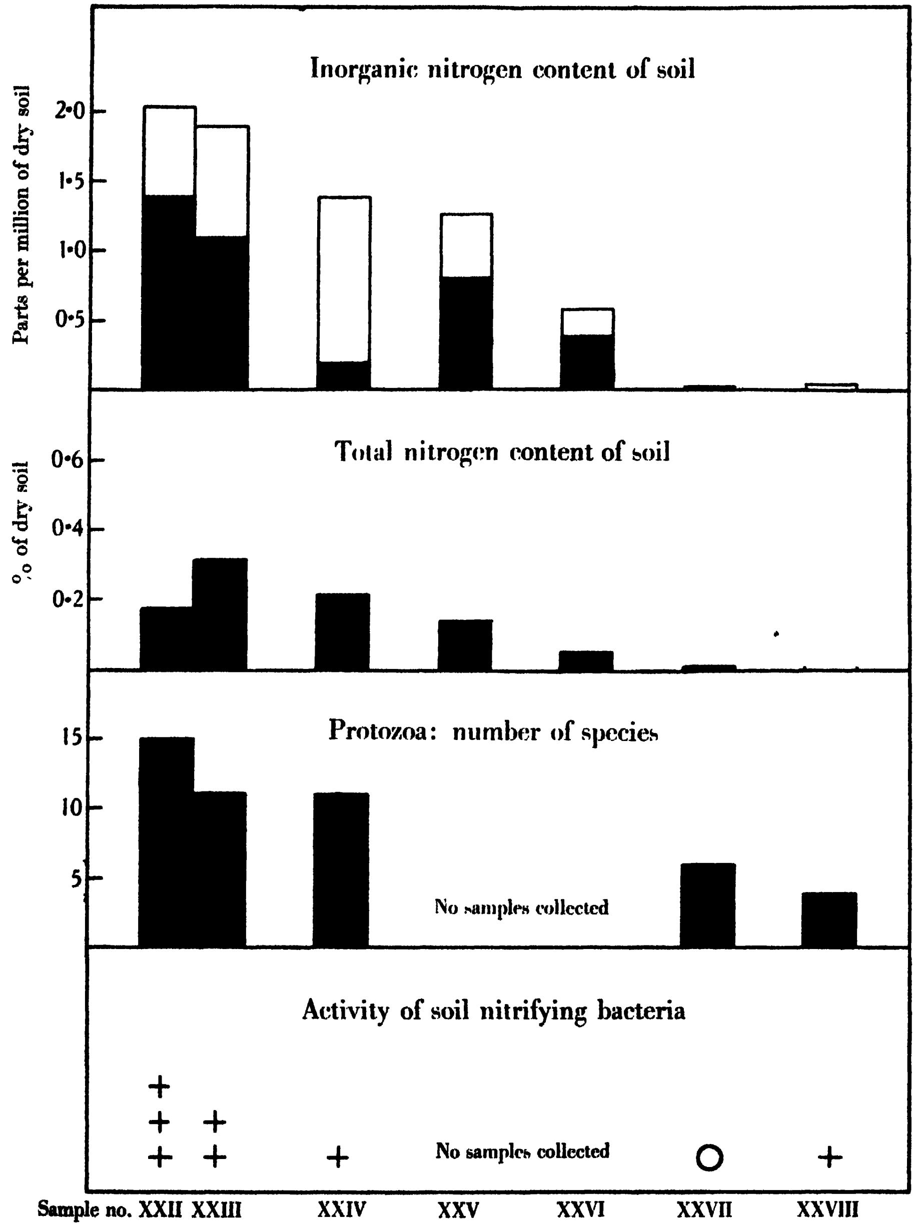

Fig. 2. Data for soil samples from slope below birdcliff at Fishburn Bay (series II). Total nitrogen expressed as percentage of oven dry soil, inorganic nitrogen as parts per million. The nitrate-nitrogen fractions are represented by the unshaded portions of the histograms. Except for a few samples when no examinations were made, the number of Protozoa species and the activity of the nitrifying bacteria are also given.

ally in its inorganic forms, and with the activity of micro-organisms, notably the nitrifying bacteria and Protozoa. The effect of bird and animal droppings on the density of vegetation, the nitrogen supply and micro-organisms is clearly shown. It is seen further that *inorganic nitrogen is extremely low* in all localities, the highest value, 2·51, being in sample XX. In the majority of localities the

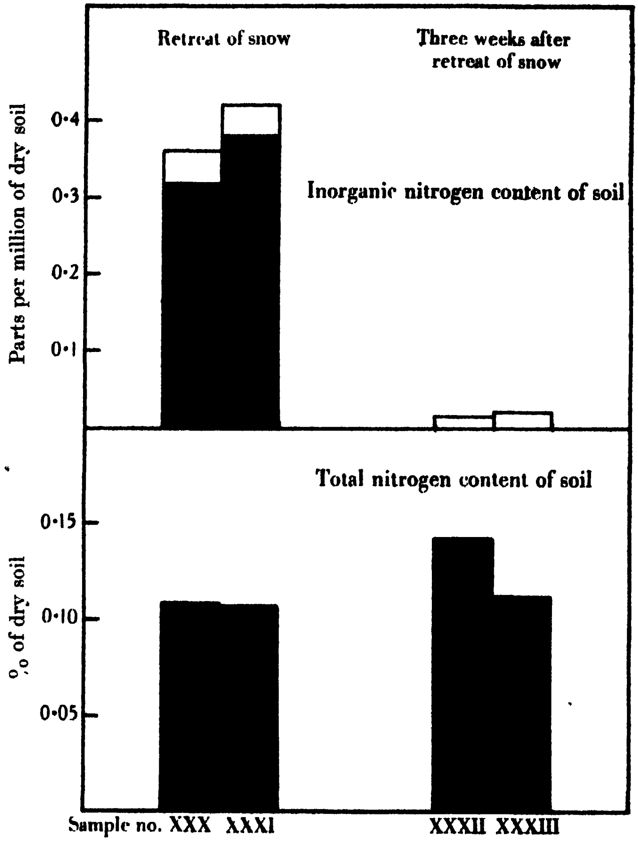

Fig. 3. Data for soil samples from a "late snow" area (series III). Total nitrogen expressed as percentage of oven dry soil, inorganic nitrogen as parts per million. The nitrate-nitrogen fractions are represented by the unshaded portions of the histograms. Except for a few samples when no examinations were made, the number of Protozoa species and the activity of the nitrifying bacteria are also given.

level is much below 1·0 p.p.m. For purposes of comparison it may be noted that in English grasslands inorganic nitrogen ranges from 10·0 to 30·0 p.p.m. (4). Since plants absorb nitrogen principally in the inorganic form it is evident from the present results that inorganic nitrogen content of the soil on Jan Mayen is extremely low, and that the type of vegetation present is related to the nitrogen level. This situation suggests extreme nitrogen deficiency but it must be borne in mind that nitrogen deficiency cannot be assessed solely on the basis of the concentration of inorganic nitrogen. The level of inorganic nitrogen in the soil represents the balance between its production by bacterial activity on the one hand and its removal by plants or by leaching on the other. It follows therefore that with the same concentration of nitrogen and the same plant covering, the degree of nitrogen deficiency will be greatest for a soil in which bacterial activity is least. Any discussion of the factors responsible for the low prevailing nitrogen level must therefore start with an examination of the effect of the environment on the soil micro-organisms.

The effect of the environment on the micro-organisms in the soil. Since low temperature is one of the outstanding features of the arctic environment from the viewpoint of soil microbiology it is appropriate first to consider its effects. It has been found in temperate regions that nitrogen fixation by *Azotobacter* is very slight below 7° C. (Koch (**5**)). Furthermore, Blackman (**2**) found that below 10° C. the growth of pasture grasses in England was limited by the rate at which organic nitrogen was broken down by micro-organisms.

Few soil temperature measurements were made on Jan Mayen, but it must be rare even in summer for the soil temperature to reach 7° C., since the mean summer air temperature is less than 6° C. For 6–8 months of the year soil temperatures are considerably below this level. Possibly the species of *Azotobacter* in the arctic have a lower temperature optimum than those in temperate regions. It is hoped that this question will be investigated, but there can be little doubt that for the greater part of the year the activity of *Azotobacter* is restricted by temperature. Some evidence that the low temperature does not entirely inhibit the activity of *Azotobacter* is however provided by a comparison of samples I and II from adjacent areas in the "volcanic desert". In the former sample micro-organisms were entirely absent and the only nitrogen was a trace of nitrite. In sample II, however, *Azotobacter* was present though other bacteria were absent, and there was a low total nitrogen value together with a scanty development of plants. The advent of *Azotobacter* was either associated with the development of conditions conducive to plant colonization, or consequent upon the growth of plants.

Nitrification has been shown to occur down to temperatures of 5° C. (Russell & Appleyard (**6**)). The degree to which the activity of nitrifying bacteria was limited by temperature on Jan Mayen cannot be gauged, though it would appear likely that during the winter months their activity was suspended. The marked activity of these organisms in sample XXXIV from a warm region near a steam vent is a further indication of the temperature effect.

The effect of temperature on ammonification may now be considered. Attention has already been directed to the absence of ammonia in all samples from the "late snow" area. In this locality the soil temperature had been 0° C. till a day before samples XXX and XXXI were taken. This suggests that ammonification may be inhibited by low temperature. Further, the presence of a comparatively high ammonia level in sample XXXIV from a specially warm locality by a steam vent supports the view that temperature may have a marked effect on ammonification. On the other hand, it should be pointed out that the occurrence of ammonification at 0° C. has been reported.

The acidity of the soil is known to have a very marked effect on the activity of bacteria. Acid conditions prevent nitrogen fixation by *Azotobacter*, but as the *p*H of all but one of the soil samples fell within the range 7·1–7·6 *p*H this factor could not have been operative.

It has been found by Sandon (8) and Sandon & Cutler (9) that the Protozoa from arctic and antarctic regions resemble those found in temperate countries. The variety of species (in all thirty-six) found on Jan Mayen support this view. The close correlation between nitrogen supply and the number of species of Protozoa present has been emphasized already, as has also the occurrence of Ciliata in localities frequented by birds or mammals. Possibly these organisms were transported by animals and deposited in their excreta.

The uptake of nitrogen by plants. The lack of nitrogen analyses of the plants growing in the various localities prevents any accurate estimate of the amount of nitrogen utilized in growth. Some evidence of the uptake of nitrogen is, however, provided by the four soil samples from the late snow area at Fishburn (samples XXX–XXXIII). The nitrogen contents are shown graphically in Fig. 3. It will be seen that all the nitrate nitrogen in the soil was removed during the period in which the plants were developing and the snow melting rapidly. After the time when samples XXXII and XXXIII were made the rate of nitrogen uptake would clearly be limited by the rate of bacterial activity, though in forms not available to plants there was still a reasonable level of nitrogen.

Attention must be drawn to the capacity of the plants for taking up nitrogen when the total level of inorganic nitrogen is very low. Blackman (2) has found in English pastures that the inorganic nitrogen content of the clay soils seldom fell below 4–5 p.p.m., the plants being unable to absorb the nitrogen when the content was below this level. The plants found on Jan Mayen, as will be seen from the diagrams, are able to reduce the inorganic nitrogen level to a markedly lower concentration.

The nitrogen in the soil. Having now examined the bacterial processes whereby the inorganic nitrogen is formed and also the behaviour of plants in removing it from the soil, it is possible to consider the nitrogen content of the soil both with regard to the total amount present and the relationship between the various nitrogen fractions. Nitrogen in the inorganic form constituted but a small fraction of the total nitrogen present. The ratio of total to inorganic nitrogen was greater than 100 in all cases, except the anomalous steam blowhole locality. In the later samples from the "late snow" area this ratio was as high as 70,000. This situation indicates that the prevailing nitrogen deficiency is due rather to the slowing down of bacterial activity than to an actual shortage of nitrogen in all forms. This very low concentration of inorganic nitrogen would, however, favour nitrogen fixation by *Azotobacter* provided that there was a supply of energy material of low nitrogen content, but the fixed nitrogen would not immediately be made available as it would be in the form of protein. Further, it should be noted that *Azotobacter* requires a large supply of available phosphate for optimal fixation to occur, and it is not known whether phosphate was a limiting factor on Jan Mayen.

It has already been suggested that the prevailing low temperatures are to a large degree responsible for the low rate of bacterial activity, but at the same time it is clear from the considerations advanced above that the supply of soil nutrients is also an important controlling factor. Thus the restricted development of bacteria in many localities is no doubt related to the low soil organic matter, which is itself due to plant growth being limited by low temperature and other climatic factors. The importance of an adequate water supply may also be mentioned, and it will be seen from the water content and loss by ignition data (Tables 1–3) that the higher water contents are generally found in the soils with the larger content of organic matter. It should be borne in mind, however, that the figures for loss by ignition give no accurate measure of the organic matter present, accordingly they have not been considered in detail. Especially in localities where mosses were growing the inclusion of much living material in the samples was unavoidable.

The importance of bird and animal excreta is evident; not only is the nitrogen content of the soil thereby raised, but also it is supplied in a form in which, through the activity of bacteria, it can readily be made available for plant growth. Furthermore, the increased nitrogen supply will facilitate the breakdown of cellulosic material, thus increasing the humus content of the soil and thereby raising its water-holding capacity; this in turn will enable a much more abundant population of micro-organisms to develop. None the less a marked degree of nitrogen accumulation is possible in particularly favourable localities where birds and mammals do not congregate. This is shown by samples XII and XIII. The situations from which these samples were taken provided particularly favourable conditions of shelter and water supply, which enabled a more abundant vegetation to develop than in the majority of localities. Thus a greater supply of organic matter was provided as a substrate for bacterial activity, and in consequence the level of both soluble and total nitrogen became in time much higher than in neighbouring, but more exposed, situations (e.g. sample IX). A similar example of a gradual increase in the soil nitrogen, resulting from conditions favouring the growth of vascular plants, is shown by samples VII and XI. These two samples were taken but a few feet apart, but the former was from an exposed slope while the latter was from a sheltered bank. In this connexion it may be noted that Starkey (**10**) has clearly demonstrated the stimulating effect of root systems on bacterial activity.

The absence of Leguminosae from arctic regions should be emphasized. No members of this family occur on Jan Mayen and, so far as the available data go, they are not present in Spitzbergen or Greenland. In many regions nitrogen fixation by the nodules on their roots is an important source of nitrogen in the soil. Thus, the non-occurrence of such plants in arctic regions is to be regarded as a contributory cause of the low prevailing nitrogen level.

Finally, the source of the nitrogen supplied to the soil in bird droppings should be considered. The sea birds derive their nitrogen from the fish they eat which in turn obtain it from the plankton. Nitrogen fixation in sea water has not been demonstrated and it must therefore be concluded that the nitrogen in sea water has been carried down by the rivers. Thus the birds return to the soil nitrogen which originated there and was removed by leaching. The soil nitrogen lost into the ocean in temperate regions is considerable. On a small arctic island, however, the large bird population together with the low nitrogen supply in the soil appear to result in the situation that the amount of nitrogen added to the soil as excreta exceeds that lost by leaching.

The nitrogen requirements of arctic plants. An examination of the data presented in this paper conjointly with the ecological description of the island (7) shows clearly that there was a marked variation in the nitrogen requirements of different species. In the localities where nitrogen was particularly deficient, mosses and lichens were often the most frequent plants. The vascular plants which did appear in these localities showed the effect of low nitrogen supply by their stunted development. Such species as *Salix herbacea*, *Oxyria digyna*, *Draba arctica*, *Halianthus peploides* and *Ranunculus glacialis* may be mentioned in this connexion.

A number of vascular plants occurred only in regions of higher nitrogen content. Among these plants *grasses* were perhaps the most important group, and attention has been drawn ((7), p. 172) to the well-developed strands of *Festuca vivipara* which were found only beneath bird cliffs. It may be noted that on Spitsbergen a similar relationship between grasses and nitrogen supply has been noted by Summerhayes & Elton (11). Other species which appeared to require a high nitrogen level were *Sibbaldia procumbens* and *Alchemilla glomerulans*. Species which grew over a range of soils of widely differing nitrogen content were characteristically more luxuriant in situations where the nitrogen level was high. This effect was shown especially strikingly by the genus *Cochlearia*. Thus it is evident that not only the density but also the floristic composition of the vegetation is largely controlled by the level of nitrogen. It follows that nitrogen supply must be regarded as a most important ecological factor in arctic regions.

It is not possible to state precisely how widely the conclusions reached on Jan Mayen can be applied to other arctic regions but, since the factors responsible for the low nitrogen level are operative throughout the arctic and it may be conjectured that when the nitrogen fractions are determined accurately in other regions, and nutritional experiments are undertaken, similar conditions of nitrogen deficiency will be established. It is of interest that Omeliansky (quoted by Waksman (**12**)) was unable to demonstrate the presence of *Azotobacter*, nitrifying or cellulose-decomposing bacteria in soils from northern Siberia (lat. 72° 15′ N.). Barthel (**1**) investigated soils from Disko and other localities on East Greenland and found *Azotobacter* in only one out of eighteen samples, while nitrifying bacteria were isolated in five cases. In the present work these organisms have been detected or isolated in a comparatively high percentage of the soils studied.

On account of the short duration of the 1938 expedition these observations are necessarily limited, and it is desirable that fuller investigations should be undertaken. More particularly the absorption of nitrogen by the vegetation deserves further investigation by systematic sampling and analyses of plants during the course of their development. From this it would be possible to determine the rate of nitrogen uptake from soils of various types and hence eventually to show the relative magnitudes of the processes of gain and loss. Moreover, the effects of the various factors involved in the process could thereby be better evaluated.

SUMMARY

1. Soil samples were collected on Jan Mayen Island from a number of localities where the vegetation was surveyed.
2. The nitrogen content of the soil, both inorganic and total, was determined. The bacteria and Protozoa were also studied.
3. The importance of bird and animal excreta in increasing the nitrogen content of the soil was demonstrated.
4. A close correlation is found between the density of the vegetation, the soil micro-organisms and the nitrogen supply. This effect is shown not only by comparing localities on various parts of the island but also by the study of a single slope where there was a gradation in the amount of bird droppings.
5. Inorganic nitrogen was everywhere at a low level, and, in situations supporting a sparse vegetation, nitrate nitrogen was nearly always absent.
6. It is concluded that in the island nitrogen deficiency is widespread and is a factor of foremost importance in determining the distribution and development of the various types of communities.
7. The effects of the environmental factors are discussed and it is suggested that a slow rate of bacterial activity, due both to low temperature and to low nutrient supply, is the main cause of nitrogen deficiency.

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PHYSIOLOGICAL AND ECOLOGICAL STUDIES ON AN ARCTIC VEGETATION

III. OBSERVATIONS ON CARBON ASSIMILATION, CARBOHYDRATE STORAGE AND STOMATAL MOVEMENT IN RELATION TO THE GROWTH OF PLANTS ON JAN MAYEN ISLAND

BY R. SCOTT RUSSELL

(*With four Figures in the Text*)

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INTRODUCTION

IN the first of this series of papers (**20**) describing the botanical results of the Imperial College Expedition to Jan Mayen a general account was given of the vegetation of the island together with the prevailing environmental conditions. The second paper (**19**) indicated a marked correlation between the vegetation, the supply of nitrogen and the micro-fauna and flora of the soil. On the basis of these results it was possible to discuss the effects of the various ecological factors, especially shelter from wind, water supply and the available nitrogen, in relation to the distribution of the different types of vegetation.

There remains for consideration in the present paper the effects of the environment on carbon assimilation, carbohydrate storage and stomatal movement.

The factors considered in the earlier papers were mainly edaphic and local in their incidence, while those to be considered here are widespread throughout the region and determine the general characteristics of the vegetation. Hence it will now be possible to compare the physiological behaviour of arctic plants with that of species in lower latitudes.

It has been pointed out already that on account of the short duration of the expedition, the results are necessarily limited. Care must be taken not to apply too widely conclusions which are based on a brief investigation in a restricted area. It is felt, however, that a consideration of the results in some detail is justified, not only as they provide data on questions concerning which little precise information is available but also because the experience gained has shown a number of ways in which detailed work could be pursued with profit in the future. The methods employed and suggestions for their improvement will therefore be stressed.

THE PLANTS STUDIED

Oxyria digyna was selected for the greater part of the work because it was one of the most common phanerogams on the island. Furthermore, it was one of the few plants with leaves of sufficient size for attachment to porometer cups for the measurement of stomatal aperture. Less detailed work was carried out on *Ranunculus glacialis*, *Polygonum viviparum* and *Taraxacum croceum*. The material has been identified by Mr A. J. Wilmott (see (**21**)) and herbarium specimens have been placed in the British Museum. Brief notes on the plants are given below.

Oxyria digyna (L.) Hill (Polygonaceae). A perennial plant with numerous fleshy roots up to 1 cm. in diameter. Leaves chiefly radical, kidney-shaped, up to 3·5 cm. in diameter but usually smaller. Petioles 3–8 cm. long. Plants several years old form clumps up to 30 cm. in width, the short perennial stems being much branched.

Polygonum viviparum L. (Polygonaceae). Perennial plant with a tuberous rootstock 1–1·5 cm. in diameter. Slender stems rarely more than 15 cm. long. Leaves narrow oblong with great variation in length of petiole. The development of viviparous seedlings was noted in several cases.

Ranunculus glacialis L. (Ranunculaceae). A perennial plant with a compact rosette of small dissected leaves. Stems usually 5–10 cm. long.

Taraxacum croceum Dahlst. (Compositae). A perennial plant with a well-developed tap root. Leaves radical, pinnatifid, 8–12 cm. long, terminating in an obvate lobe. The specimens from Jan Mayen are in certain respects dissimilar to material of this species from Scandinavia, but, pending detailed study, they are referred to this species.

CARBOHYDRATE METABOLISM

The considerations which led to the selection of carbohydrate metabolism for special study have already been outlined (**20**), but it will be convenient to recapitulate them. The growing period in the arctic is short and the prevailing temperature low while light is continuous but for much of the time and especially at night it is of low intensity ((**20**), Table 3). These conditions are markedly dissimilar from those under which temperate plants develop, and varying opinions have been advanced as to their effect on the synthesis of carbohydrates. The work of Kostytchew *et al.* (**14**) and Muller (**15**) indicated that the assimilation rates of plants in the arctic are as high as in temperate regions. Wager (**25**), on the other hand, postulated that carbohydrate starvation was an important factor in controlling the development and survival of young plants in certain habitats in East Greenland. To determine whether in fact arctic plants are deficient in carbohydrates chemical analyses were carried out on material from Jan Mayen. Furthermore, an approximate method for measuring the rate of assimilation was employed and diurnal variations were also examined.

Methods of investigation

The procedure for preserving samples and determining the concentration of sugars was that described by Archbold (**1**) and Van der Plank (**24**). Immediately after collection the samples were boiled in 95% alcohol for 10 min. to ensure the inactivation of enzymes. The volume of alcohol was such that the final concentration of alcohol was about 70%. The tubes or bottles containing the samples were then sealed and brought home for analysis.

For sugar determination water extracts were prepared. The alcohol in which the material had been preserved was decanted off. The material was washed with a small quantity of alcohol and then refluxed for 4 hr at 100° C. with about 40 c.c. alcohol per g. dry weight. When the material consisted of thick roots it was pulverized in a mortar before extraction. After the above treatment the various alcohol fractions together with the washings were evaporated under reduced pressure at 30–38° C. and the residue was taken up in water and made up to volume. To prevent bacterial action the aqueous extracts were covered with a thin layer of toluene. The alcohol-insoluble material was dried at 100° C., weighed and subsequently used for starch determination.

Total sugar was determined in the aqueous extracts by the copper reduction method outlined by Van der Plank (**24**), $N/5$ sulphuric acid being employed to hydrolyse the non-reducing sugars. In some cases reducing sugars were estimated separately.

The starch in the alcohol-insoluble residues was hydrolysed with takadiastase in the following manner. The dried alcohol-insoluble material was ground with washed quartz sand and a small quantity of water, the cellular structure being thus disrupted. The resultant paste was then transferred to a convenient vessel with a known quantity of water, and placed in a boiling water bath for 1 hr. to gelatinize the starch. The extracts were then cooled to room temperature and water added to compensate for that lost during heating.

Sufficient of a 0·6 % taka-diastase (Parke-Davis preparation) solution was then added to yield a concentration of 0·05 % in the extract. After the addition of a few drops of toluene to prevent bacterial contamination, the extracts were incubated for 22 hr. at a temperature of 39° C. The solid material was then filtered off, washed, and the extracts made up to volume for the determination of reducing sugars by the copper-reduction method. Blank determinations were made with 0·05 % taka-diastase in distilled water. The amount of starch initially present was calculated by reference to a calibration curve for the hydrolysis of pure starch under similar conditions. After washing, the residual material was treated with iodine, and in no case was there any evidence of incomplete hydrolysis of the starch.

It must be noted that taka-diastase is not altogether specific for starch and that a certain over-estimation may therefore have occurred.[1]

All samples were replicated and in the majority of cases they were made up of a large number of plants. Thus the effects shown are not due to individual variations between plants. The results have usually been expressed as percentages of the alcohol-insoluble material, this basis having been chosen in preference to percentages of fresh weight on account of fluctuations of water content. For convenience the total of sugar and starch is here stated as "total carbohydrate". The difference between total and reducing sugars gives an approximate measure of sucrose.

The rate of assimilation of Oxyria digyna

The advantages of methods of growth analysis described by Briggs *et al.* (**3**) for the estimation of the rate of assimilation has been emphasized by Gregory (**6**, **7**), and the value of work of this type in the study of ecological problems has been pointed out recently (**11**). To carry out such investigations was, however, impossible on a short expedition, since a large number of plants of comparable age are required in addition to facilities for drying and weighing considerable quantities of material. Methods depending on gasometric estimation of the changes in the carbon dioxide content of the air were also impracticable. Accordingly, the rate of assimilation was determined from the increase in carbohydrate in detached leaves. Under these conditions translocation of the products of assimilation was prevented and in consequence they accumulated in the leaves. The validity of the method depends on the assumption that all the assimilate remains in the form of carbohydrate. As it was found that no increase in alcohol-insoluble material occurred in detached leaves of *Oxyria digyna* it appears likely that this condition was realized although it is possible that part of the assimilate was in the form of organic acids. The measures of assimilation here obtained are consequently minimal. No great accuracy is claimed for the method but the simplicity of the field technique makes it most convenient for expedition use.

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[1] Hanes (**10**) found that when taka-diastase was used to hydrolyse apple starch consistently higher estimates of starch were obtained than when the hydrolysis was carried out with β-amylase. In many of the samples here studied starch values were extremely low but the presence of starch and its hydrolysis by taka-diastase were definitely shown by testing with iodine. In these cases any substance other than starch which was hydrolysed by taka-diastase could have been present only in negligible quantities. In samples where higher starch figures were obtained there was a possibility of greater errors.

Two experiments of this type were attempted at different times in the season. Unfortunately the leaves used in the earlier and more detailed investigation were devoured by the pigs of the Jan Mayen Meteorological Station towards the end of the experiment. The results of the second experiment are presented in Table 1.

Table 1. *Assimilation (mg. per leaf) of detached leaves of* Oxyria digyna. *Six-day period*

	Starch	Reducing sugar	Total sugar	Total carbohydrate
Initial sample	0·82	0·95	1·61	2·43
	0·89	0·95	1·79	2·68
Final sample	0·71	6·46	9·86	10·57
	0·33	6·57	10·39	10·72

Mean increase in total carbohydrate: 8·09.

Approximate net assimilation rate: 0·30 g. per sq. dm. per week.

For this experiment two hundred healthy leaves of *O. digyna* were detached at the base of their petioles and were divided into four comparable sets. Two of the samples were preserved immediately for carbohydrate determination and the remainder were kept in the open for 6 days with their petioles in wet sand, under which conditions they did not wilt. At the conclusion of the experimental period the leaves were preserved for analysis. It will be seen from Table 1, where the results are shown as mg. per leaf, that there was a large increase in total sugar during the period of the experiment, while a small decrease in starch occurred. No precise measure of leaf area was made, but an approximate value has been derived from other and comparable material and on this basis the *net assimilation rate* has been calculated as 0·30 g. per sq. dm. per week. This estimate is to be regarded as minimal, not only for the reasons set out above but also because the experiment was carried out late in the season (15–20 August), when light intensity, especially at night, was greatly reduced as compared with the earlier part of the season ((**20**), Table 3), and when, moreover, the plants were senescent. Furthermore, it is likely that the assimilation rate decreased during the 6 days of the experimental period. In investigations of this type it is desirable to reduce the experimental period as far as possible. The analytical methods are sufficiently accurate to give reliable results with an experimental period of 2 or 3 days, while still shorter periods could be used if the number of leaves per sample (fifty in the present experiment) was increased.

Seasonal changes in the carbohydrate content of Oxyria digyna

The beginning of the growing season in arctic regions is determined primarily by the time at which the snow retreats. Thus although the present investigations were not started until July, when plants in the majority of lowland localities were well grown, plants in areas from which the snow was just retreating were still at early stages of development. A few such areas remained till mid-August ((**20**), p. 169). It was therefore possible, by taking samples from different localities, to trace the seasonal drift in carbohydrate.

Table 2. *Seasonal changes in the carbohydrate content of* Oxyria digyna. *Results expressed as percentages of the alcohol-insoluble material*

Young plants

	Roots		
	Starch	Total sugar	Total carbohydrate
A. Plants at edge of retreating snow	2·19	34·24	36·43
	1·59	38·96	40·55
B. Plants uncovered for 3 weeks and now in flower	3·71	22·00	25·71
	2·69	23·60	26·29

Mature plants

	Tops			Roots		
	Starch	Total sugar	Total carbohydrate	Starch	Total sugar	Total carbohydrate
C. 21 July, plants in fruit	5·45	7·82	13·27	5·83	14·56	20·39
	4·16	6·45	10·61	6·13	10·23	16·36
D. 19 August	6·12	17·02	23·14	13·93	17·38	31·31
	5·64	19·57	25·21	9·18	12·07	21·25
	4·69	18·63	23·32	15·71	15·50	31·21
	6·00	22·55	28·55	13·35	10·33	23·68

In Table 2 are shown the carbohydrate contents of plants of *O. digyna* at four stages in the growth cycle. The results are represented graphically in Fig. 1. The first two samples were taken from a "late snow" area in Fishburn Valley, and the latter ones from an open area at Jameson Bay where the snow had retreated early in the season. It would have been more satisfactory if all the material could have been collected from one locality, and the possibility of local differences must be borne in mind when considering the results. Replicated samples of roots were taken on each occasion, but tops (including leaves and stalks) were collected only in the last two samples. The leaves were too small to sample at the first collection but they were well developed when the second root sample was made. It is pertinent to point out that in *O. digyna* the large fleshy roots serve as important storage organs, and form the major portion of the perennial plant. It was impossible to excavate complete root systems, and few roots of less than 2 mm. were included in the samples so that little of the tissue was of the current season's growth.

The first sample (sample A, Table 2) was taken within a day of the retreat of the snow. Only a few small leaves (which had opened under the snow covering) were present. The carbohydrate content of the roots at that time was high, averaging rather more than 38 % of the alcohol-insoluble material, but only 1–2 % was starch. After the retreat of the snow growth was rapid and plants flowered after being uncovered for only 3 weeks. During this period the carbohydrate content of the roots decreased (sample B, Table 2) to about

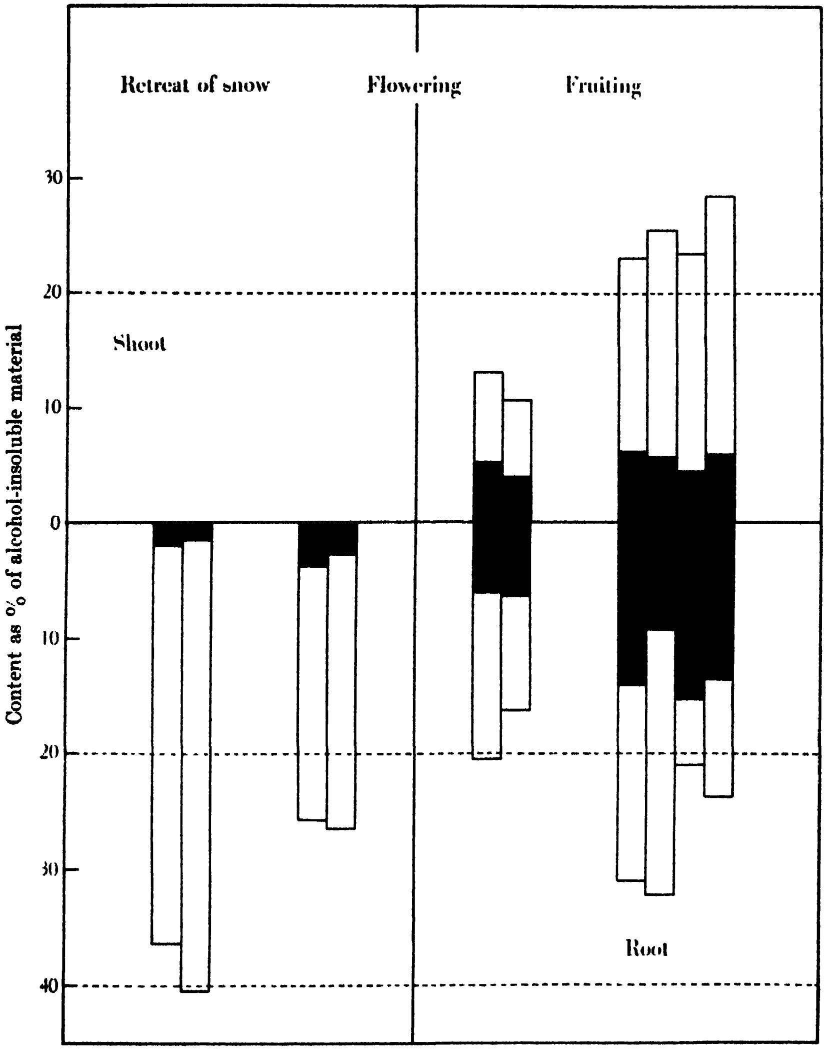

Fig. 1. Carbohydrate content (percentage of the alcohol-insoluble material) of the shoot and roots of *Oxyria digyna* at different growth stages during the season. Starch is represented by the heavily shaded parts of the columns and sugars by the unshaded sections.

two-thirds of the initial value but there was still an abundant reserve (26%). The decrease was entirely in the sugars, there being a small increase in starch. In sample C at the time of fruiting a further reduction in total carbohydrate was found in the roots though starch had again increased. In the final sample (sample D) of mature plants towards the end of the growing season, there was a large increase of carbohydrate, especially starch. From the two samples of tops it appears that in the latter part of the season sugars increased considerably while the starch level remained almost unchanged.

The following conclusions emerge: (i) At no time during the growing season was there any shortage of carbohydrate in the roots, the lowest value being 16%. (ii) At the beginning of the growing season reserves of carbohydrate are utilized in growth and towards the end of the season, after fruiting, the reserves are again built up. (iii) Early in the season the concentration of starch in roots is low and gradually increases as the summer advances. This increase continues even when the total carbohydrate level is declining. Thus it appears that during the winter, when the soil temperature is 0° C. or lower, starch is converted into sugar. The temperature in the summer is apparently sufficiently high for the reverse process to take place. The effect of temperature on the various sugar fractions is considered further on p. 305.

Diurnal changes in the carbohydrate content of leaves of Oxyria digyna

One investigation of diurnal changes in carbohydrate was undertaken late in the season (15–16 August). The light intensity at night was then very low, so that the diurnal changes were presumably greater than earlier in the season when light intensity varied less throughout the 24 hr.

Samples were taken in triplicate every 4 hr., and at the same time light intensity and temperature were measured. To reduce sampling errors each sample was made up of one leaf from each of fifteen clumps of *O. digyna*. The results are given in Table 3. Statistical analysis shows that the diurnal changes in reducing sugar, total sugar and starch were all significant. In Fig. 2 both the data and the magnitudes of the significant differences of the means are represented graphically. For convenience light intensity has been plotted on a logarithmic scale.

At the time the experiment was carried out total sugar was accumulating in the leaves (see Table 2, samples C and D) and the diurnal experiment shows that a significant increase occurred between 8.15 a.m. and 4.15 p.m.; the small drop during the night was not significant. The maximum reducing sugar value occurred at 8.15 p.m. and the minimum at midday. The diurnal changes in starch were markedly greater, and of higher statistical significance than those either in reducing or total sugar. During the night starch values declined, the minimum being reached at 8.15 a.m., after which time there was a considerable increase in starch.

Table 3. *Diurnal variations in the carbohydrate concentration of leaves of* Oxyria digyna. *Results expressed as percentages of alcohol-insoluble material.* 15–16 *August* 1938

Time	° C.	Light intensity (ft.-candles)	Starch	Reducing sugar	Total sugar	Total carbo-hydrate
8.15 p.m.	6·4	50	8·28	12·51	14·07	22·35
			6·88	13·75	20·09	26·97
			8·27	14·58	19·00	27·27
12.15 a.m.	6·4	2·5	3·86	11·97	17·48	21·34
(midnight)			1·21	12·47	18·54	19·75
			5·81	10·03	15·40	21·21
4.15 a.m.	6·6	10	0·45	12·83	18·06	18·51
			2·14	11·70	17·07	19·21
			2·67	12·04	16·56	19·23
8.15 a.m.	6·9	525	0·05	12·10	16·68	16·73
			1·00	11·31	18·18	19·18
			0·05	11·09	16·09	16·14
12.15 p.m.	10·2	1375	3·04	10·92	17·82	20·87
(noon)			1·50	8·91	19·33	20·83
			3·95	10·43	16·82	20·77
4.15 p.m.	10·0	1050	5·05	11·20	21·38	26·43
			4·61	13·24	26·16	30·77
			3·64	12·74	21·97	25·61

Statistical analysis of carbohydrate values *v.* occasion

	"Z"	5·0% point	1·0% point	Significant difference of means
Starch	1·232	0·553	0·811	2·234
Reducing sugar	0·798	0·553	0·811	1·627
Total sugar	0·788	0·553	0·811	3·350

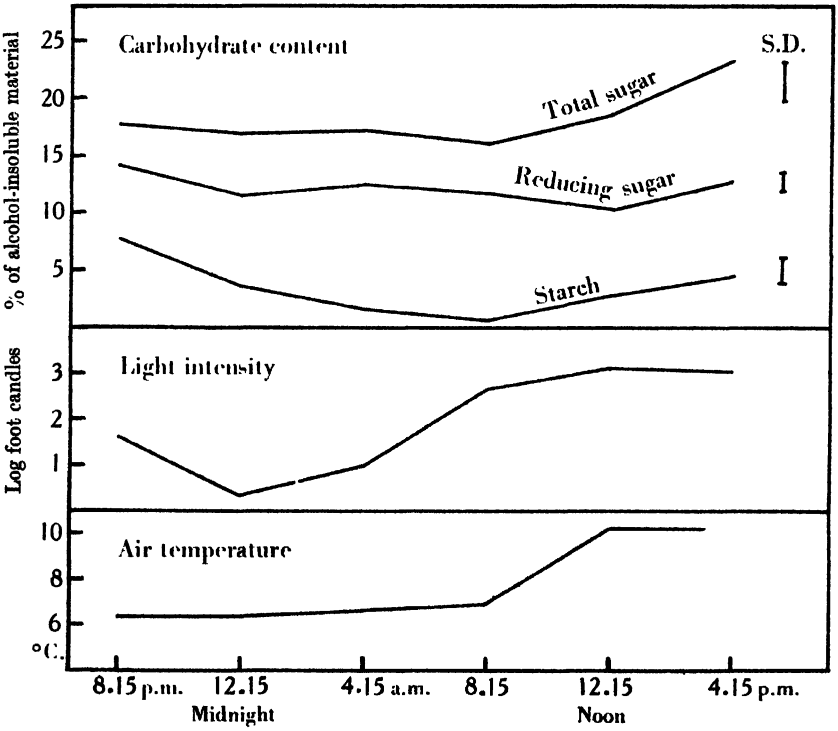

Fig. 2. Diurnal changes in the carbohydrate content (percentage of alcohol-insoluble material) in the leaves of *Oxyria digyna*. Significant differences ($P = 0·05$) between pairs of the mean carbohydrate values are shown.

Without the necessary data from which the variation in translocation can be assessed it is not possible to determine the true assimilation rate. It appears however that the concentration of starch especially is correlated with assimilation. During the night, when assimilation is reduced by the lowering of light intensity and temperature, starch decreases, while conversely the starch values rise after 8.15 p.m. when light and temperature are increasing.

Other observations

In addition to the above investigations on the carbohydrate content of *Oxyria digyna* a few determinations were made on *Polygonum viviparum* and *Ranunculus glacialis*. The results are shown in Tables 4 and 5.

Table 4. *Carbohydrate content of* Polygonum viviparum. *Results expressed as percentages of alcohol-insoluble material*

	Tops			Roots		
	Starch	Total sugar	Total carbohydrate	Starch	Total sugar	Total carbohydrate
Sample I, 16 July	—	—	—	11·32	11·71	23·03
	3·01	5·16	8·17	12·17	12·25	24·42
	3·16	11·33	14·49	12·13	8·11	20·24
	3·78	9·56	13·34	—	—	—
Sample II, 15 August	1·02	6·06	7·08	—	—	—
	1·41	5·68	7·09	9·03	6·12	15·15
	0·63	6·69	7·32	16·93	8·09	25·02
	1·59	7·02	8·61	9·54	8·06	17·60

Table 5. *Carbohydrate content of leaves of* Ranunculus glacialis *on* 19 *July. Results expressed as percentages of alcohol-insoluble material*

Starch	Reducing sugar	Total sugar	Total carbohydrate
7·95	31·44	46·44	54·39
8·27	30·53	41·39	49·66

Polygonum viviparum was sampled on two occasions, 16 July and 15 August, both series of samples being made in the same locality in the Fishburn Valley. Roots and tops were analysed separately and in Table 4 the figures on each horizontal line refer to the roots and tops of a single sampling. Three samples were lost in transit. While there is considerable variation between replicates there is a general decrease in the level of starch in the tops between the first and second samples. In the roots on the other hand there is some indication of a decrease in sugars. The general lowering of the carbohydrate level was presumably due to fruiting which took place in the interval between the two collections. Without a full series of samples at different times in the season it is obviously not possible to discuss in detail the seasonal changes in carbohydrate. It is important however to note that a considerable amount of carbohydrate was present although the general level was lower than that in

Oxyria digyna. Replicated determinations of carbohydrate in the leaves of *Ranunculus glacialis* were made on one occasion only (Table 5), and again very high concentrations were found, on the average over 50%, and of this the greater part was reducing sugar.

OBSERVATIONS ON STOMATAL MOVEMENT

Special interest attaches to the behaviour of the stomata of arctic plants on account of the continuous illumination in summer. Previous observations, made by infiltration methods (**15**), indicated that in some plants the stomata were wide open continuously, while in others the aperture varied with light intensity. While such methods give a general indication, they do not permit an accurate measurement of stomatal aperture and a direct comparison of different species is therefore impossible. More precise observations may however be made by means of the resistance porometer which permits continuous observations to be made of the resistance of the stomata to air flow. The utility of such instruments on an expedition is restricted on account of the fragility and complexity of the apparatus required. With due care it has however been found possible to use this method in the field.

Methods of investigation

The principle of the resistance porometer has been described fully by Gregory & Pearse (**9**) and only a brief outline of the method is necessary here. A stream of air is drawn through the leaf into a small cup by means of a constant pressure aspirator, the connexion between the leaf and cup being rendered gas-tight by a gelatine washer. A manometer is attached to the system between the cup and the aspirator and the air stream is caused to pass through a standard capillary resistance before reaching the aspirator. The resistance of the stomata in the portion of the leaf attached to the cup bears a simple relation to the ratio between the pressure registered in the manometer and the pressure in the aspirator, and from these data the resistance of the leaf may be calculated in terms of the known resistance. Hence by reading the manometer from time to time, changes in the flow resistance of the stomata may be determined and expressed in the conventional units of resistance defined by Gregory & Pearse (**9**).

For use on Jan Mayen it was necessary to make the apparatus as portable as possible, and for this reason the delicate glass parts were built into stout oak boxes. Quart milk bottles served as suitable aspirators and were mounted on a small folding wooden stool pegged to the ground, brackets being attached to the legs of the stool to support the necessary glass tubing. The apparatus was housed in a small tent backing on the slope on which the plants under observation were growing. Tubes were run out beneath the walls of the tent to the cups attached to the plants. For the greater part of the time three sets of apparatus were employed simultaneously.

Certain difficulties were experienced; the high humidity of the atmosphere caused swelling of the gelatine washers with which the leaves were attached to the cups. This was however largely overcome by smearing the washers with a beeswax-paraffin grease. In foggy or wet weather moisture condensed on the upper surface of the leaves sealing the stomata, but it was found that a celluloid screen fixed some distance from the leaves overcame this to some extent.

The experimental procedure was as follows. A cup was attached to a healthy leaf without injury to either the lamina or the petiole, the aspirator was set running and the apparatus tested for leakage. After an initial period to enable the leaf to recover from such slight shock as may have occurred in setting up the apparatus, the manometer was read and in addition the temperature and light intensity were measured with a Weston photronic cell (model 594). The relative humidity was also determined by means of a whirling hygrometer, but as the atmosphere was almost always above 90% of saturation these data will not be presented here. Observations were made every 4 hr. during a 24 hr. period. *Oxyria digyna* and *Taraxacum croceum* were alone used in the investigations, as the majority of other species had such small leaves that they could not be employed conveniently.

Results

In examining the results it is necessary to bear in mind the complexity of the factors, both internal and external, which affect stomatal movement. Temperature, light intensity, wind and atmospheric humidity are the most important external factors. In the investigations here reported plants were studied in their natural environment and in consequence the various factors which affect stomatal movement were uncontrolled. Without a knowledge of all the factors operative a full interpretation of the results is impossible. At present only a partial explanation of the results in terms of temperature and light intensity can be advanced.

A considerable number of experiments were performed but of these only a few merit consideration. Owing to the high prevailing winds leaves rigidly attached to porometer cups were liable to become damaged during the course of an experiment, while in other cases the swelling of the washers or the condensation of moisture already noted was a cause of failure. Unfortunately such accidents were fairly frequent.

A selection of results from successful experiments is shown in Figs. 3 and 4. In each figure stomatal resistance is plotted against temperature and the logarithm of light intensity measured in foot candles. Stomatal resistance is plotted towards the origin on account of the association of low resistance (i.e. wide open stomata) with high light and temperature. Light intensity is again plotted on a logarithmic scale. Fig. 3 is for *Oxyria digyna* and Fig. 4 for *Taraxacum croceum*.

The diagrams show that stomatal behaviour is somewhat erratic and by no means completely controlled by light or temperature but the following

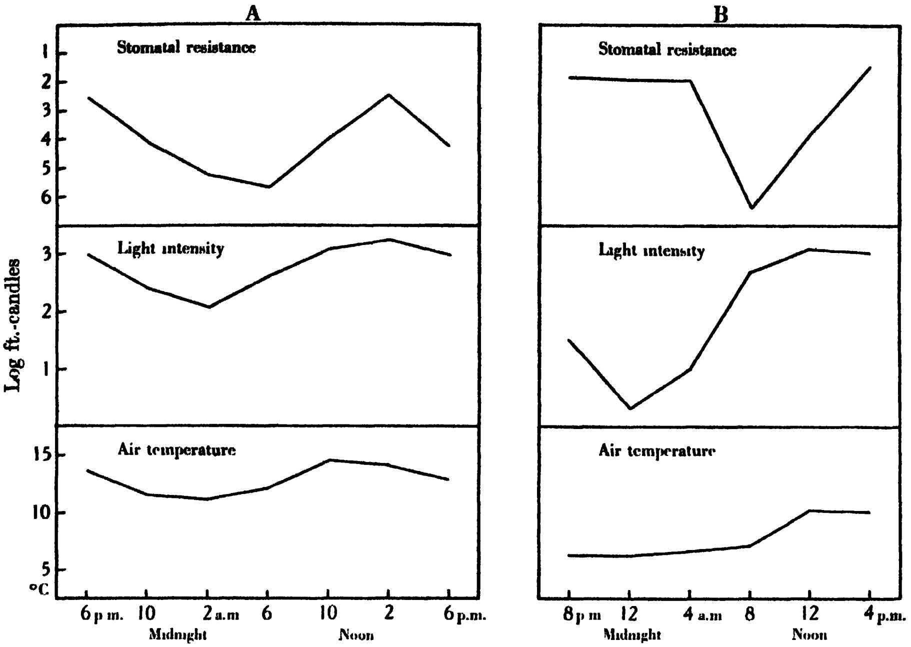

Fig. 3. Stomatal resistance to air flow of *Oxyria digyna*. A, 9–10 July; B, 15–16 August.

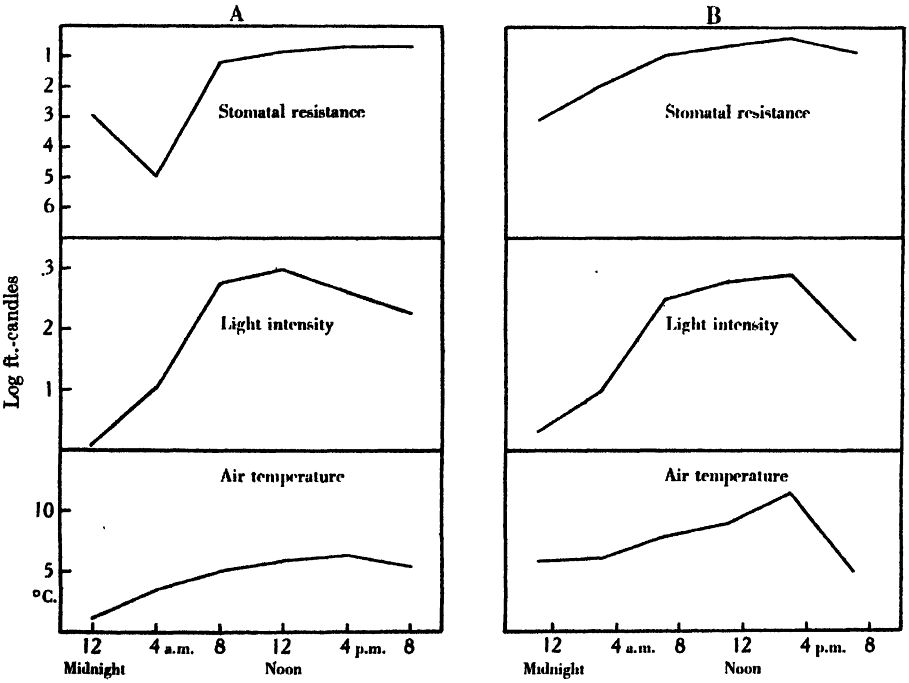

Fig. 4. Stomatal resistance to air flow of *Taraxacum croceum*. A, 17 August; B, 19 August.

conclusions may be drawn: (i) The stomata were always open although the aperture varied from time to time during the day. (ii) The stomata were more widely open when light intensity and temperature were high. This is particularly well shown in Figs. 3 and 5. Since light intensity and temperature are correlated it is not possible to state which factor exerted the more important effect on stomatal movement. There was a marked time lag—the stomata being most closed several hours after the minimal light and temperature values were recorded. (iii) There is no evidence of change in stomatal behaviour as the season advanced and the light intensity at night decreased. This is shown by comparing Figs. 3 A and 3 B for experiments carried out on 9–10 July and 15–16 August respectively. In the former the minimal light intensity was 100 ft.-candles while in the latter it was only 2·5 ft.-candles. (iv) The stomatal resistance of *Oxyria digyna* was somewhat greater than that of *Taraxacum croceum*, but there was a general similarity between the behaviour of the two plants.

These conclusions are borne out by the results of other experiments, and the calculations of stomatal resistance are confirmed by measurements of the amount of water passing out of the constant pressure aspirator, which gives an alternative estimate of the mean stomatal aperture during the intervals of time between readings.

It has been sufficiently established that the stomata of the plants studied show a positive response to light intensity and temperature, but it is highly desirable that more extensive work should be undertaken. The length of time required for field work of this type militates against the successful application of these methods on a short expedition. Simple and rapid technique is desirable, and the stripping method of Lloyd by which the epidermis is removed and preserved in absolute alcohol for subsequent microscopic examination would appear to have very definite advantages.

Discussion

The investigations made were concerned primarily with an ecological problem, namely, the effect of the arctic environment on certain of the metabolic processes which control the growth and development of the vegetation. In considering the results this aspect will be emphasized.

(1) *The effect of the arctic environment on carbon assimilation*

The rate of assimilation. For the purposes of the present discussion *net assimilation rate* is the most satisfactory measure of assimilation. It may be defined as the increase in dry matter per unit leaf area per unit time and it is therefore a direct measure of carbon accumulation, respiration losses being disregarded. For the reasons already indicated the most satisfactory estimates of net assimilation rate are derived from the analysis of growth data. So far as the writer has been able to ascertain no systematic study of assimilation by growth analysis methods has been carried out in arctic regions. Gasometric methods were employed by Kostytchew *et al.* (**14**) on the Murmansk coast of northern Russia, and by Müller (**15**) at Disko, West Greenland. Both localities are at the latitude of about 69° N. Kostytchew *et al.* reported higher assimilation rates for a 24 hr. period than are found in temperate regions. Müller, who carried out numerous experiments on *Salix glauca* and *Chamaenerium latifolium*, found assimilation rates within the same range as those of temperate plants. Unfortunately, he worked at artificially controlled temperatures considerably above the mean summer temperature of the region. His observations on the interaction of light and temperature affecting assimilation are discussed below. The single experiment on assimilation reported in this paper gives a net assimilation rate of 0·30 g. per sq. dm. per week for a detached leaf. For the reasons already stated this is a minimal value and much higher values may occur earlier in the season. It has been shown by Heath & Gregory (**11**) that over a wide range of annual plants in different localities net assimilation rates are remarkably constant under normal conditions, and approximate to a mean value of 0·55 g. per sq. dm. per week. It would be premature to state whether a similar level obtains in arctic plants. The small amount of data at present available suggest however that, during the most active period of growth, the net assimilation rates of arctic plants are at least comparable with those of plants in temperate regions.

The effect of light and temperature on assimilation. Several workers have found that assimilation is continuous throughout the period of the arctic summer when light is continuous (Kjellerman (**13**), Curtel (**4**), Fries (**5**), Müller (**15**)). Curtel suggested that the rate of assimilation was minimal when light intensity was lowest and this has been confirmed by Müller. The diurnal changes in carbohydrate content shown in the present investigation also indicate a diurnal change in the rate of assimilation and in this connexion the observations on stomatal movement are of interest. The stomata of *Oxyria digyna* and *Taraxacum croceum* were never completely shut but they were less widely open when light was low. Müller who used infiltration methods obtained similar results with several species. In certain other plants however (e.g. *Salix glauca* and *S. herbacea*) he found that the stomata were always fully open.

The duration of the period in which assimilation is continuous is determined both by the light intensity at midnight and by the temperature. The interaction of light and temperature has been studied by Müller (**15**). He found that the "compensation point" was depressed by lowering the temperature. This is because the temperature coefficient of respiration ($Q_{10°}$) is higher than that of real assimilation. The "compensation points" which Müller found are quoted below (the values for 0° C. were derived by interpolation):

	20° C.	10° C.	0° C.
Salix glauca	156	69	23 ft.-candles*
Chamaenerium latifolium	143	46	16 ,,

* Müller's results have been converted from Lux to foot-candles.

It follows that at low light intensity a reduction in temperature may lead to an increase in net assimilation rate. Müller found that the net assimilation rate of *Salix glauca* was greater at 10° than at 20° when the light intensity was 370 ft.-candles or lower. For *Chamaenerium latifolium* the same relationship held when the intensity was 830 ft.-candles. Müller's findings have been confirmed by Stålfelt (**22**, **23**) who studied a number of mosses and lichens. At considerably higher light intensities (1470 ft.-candles) he found that the growth of the lichen *Evernia prurastri* was the same in plants constantly illuminated at 0° C. as in plants illuminated with light of the same intensity for 12 hr. at 15° C., thus demonstrating the effect of temperature on assimilation under these conditions as well as the importance of continuous light for growth in arctic regions.

It therefore appears that assimilation may proceed, though at a low rate, in arctic plants when both temperature and light intensity are low, and it is of interest to note that there is evidence that plants can assimilate under a covering of snow. The fact that leaves can develop even under a considerable depth of snow is well known and was observed on Jan Mayen. Polunin (**17**) found evidence of increased carbohydrate content in leaves of plants beneath 5 cm. of snow. Under these conditions light intensity is greatly reduced (cf. (**20**)). The interaction of temperature and light (both its intensity and duration) is of paramount importance in the development of arctic plants and the above considerations show that the two factors cannot be considered separately.

(2) *The level of carbohydrate within the plant*

The concentration of carbohydrate within a plant is of considerable ecological significance. Stored carbohydrates represent the excess of the products of assimilation over that required for growth (**2**). A high concentration of sugars therefore indicates that photosynthesis is proceeding at a rate in excess of that necessary to supply the requirements of respiration and metabolism, while very low concentrations indicate the reverse. Almost all plants growing in full light in temperate regions synthesize carbohydrate beyond their requirements, and large amounts of carbohydrate may be formed which are not utilized at any stage in the life history of the plant.

The data here presented (Tables 2–5) show high concentrations of carbohydrate. In *Oxyria digyna*, which was studied at several stages in the growing season, considerable reserves were present at all times (Table 3), and were depleted to the extent of only 30 % of the total carbohydrate during the period of most rapid growth. A remarkably high level of carbohydrate was found also in *Ranunculus glacialis* (Table 5). The results indicate that at any rate in these arctic plants the situation is similar to that found in temperate regions, namely, that the carbohydrate produced by assimilation is ample for the requirements of the plants under the prevailing conditions. The slow rate of growth in the arctic is therefore not due to deficiency in the supply of carbohydrates. Unfortunately little work has yet been done on this subject and it would be very desirable to confirm the present results by observations over a greater range of species and on plants of different ages elsewhere.

It has however been postulated by Wager (**25**) that carbohydrate starvation may occur in juvenile plants in *fjaeldmark*. This suggestion, unsupported by analytical data, was put forward to explain the slow growth rate and high death-rate of young plants observed by him in such habitats at Kangerdlugssuak, East Greenland (lat. 68° 30′ N.). The results here presented give no support to this hypothesis. It is true that the present observations were made on mature plants and that some, but not all, were from habitats dissimilar from those examined by Wager. There is, however, no evidence that the level of carbohydrate is lower in young plants in *fjaeldmark* than in other situations. On the contrary, a higher carbohydrate level might be expected since it appears likely that the rate of growth is depressed more markedly than the net assimilation rate by the conditions of the *fjaeldmark*. In these situations temperature is somewhat lower and the exposure to wind is much greater than in the more sheltered situations which support more luxuriant vegetation. It has been pointed out above that with low light intensities (and these are of common occurrence in the Arctic), the temperature coefficient for net assimilation rate is small or may be negative. In consequence comparatively small differences in net assimilation rate are to be expected between one situation and another in the same locality. On the other hand the rate of growth is depressed greatly both by low temperature and exposure to wind. Thus less carbohydrate will be required for growth in exposed situations and since the supply is decreased to only a small degree, increased accumulation will result. Furthermore, there is positive evidence of extreme nitrogen deficiency, especially in exposed situations where the vegetation is sparse on Jan Mayen (**19**). The conditions responsible for the low nitrogen level are no doubt operative equally at Kangerdlugssuak as on Jan Mayen in the same latitude. Nitrogen deficiency as is well known leads to accumulation of carbohydrates (Gregory (**8**)) and for this reason also a high level of carbohydrate is to be expected in *fjaeldmark* plants. *It may therefore be concluded that there is no evidence that carbohydrate starvation occurs in arctic plants. On the contrary, the evidence points in the opposite direction.*

There is at present insufficient data to discuss in detail the interesting problems of seedling survival raised by Wager; but it would seem possible that mechanical damage, due to the soil movements associated with freeze-thaw processes, may be in part responsible for the high mortality of seedlings recorded in open situations.

Before leaving the question of carbohydrate storage the ratios of the various carbohydrate fractions may be examined. A high ratio of reducing sugar to total sugar is shown in each case, the values being 0·63 (Table 1) and 0·64

(Table 3) for the leaves of *Oxyria digyna*, and 0·71 (Table 5) for the leaves of *Ranunculus glacialis*. Without comparable data for the same plants in different climates it is not possible to determine whether temperature affects this ratio. It may be noted that different species in temperate regions can show widely differing ratios (cf. Onslow (**16**)). The effect of temperature on starch formation is more obvious. In the roots of *Oxyria digyna* there was a steady increase in starch during the summer even when total carbohydrate was decreasing. During the winter almost all the starch was converted into sugar, no doubt as a result of the low temperatures. This observation is in agreement with findings of Hopkins (**12**) who showed that below 4·5° C. the starch present in potatoes was converted into sugar. The mean summer temperature of Jan Mayen is only 1·5° C. above this level and it would be of great interest to know if higher starch ratios are found in the species studied when they are growing in temperate localities.

(3) *Factors controlling the growth of arctic plants*

The effect of the short growing season. No systematic study of growth rates has been made in arctic regions, and from such fragmentary data as are available it is possible to say only that in general growth rates are low. Development does not occur at a uniform rate throughout the summer. At the beginning of the season the production of leaves is extremely rapid and flowering may occur within 2 or 3 weeks of the retreat of the snow. During the latter part of the season reserves are built up to be utilized in the next year's growth. Annual plants are uncommon in arctic regions; *Koenigia islandica* is the sole representative on Jan Mayen. It would appear that perennial plants with a capacity for storing carbohydrates are specially suited to arctic conditions, since the reserve material enables them to develop rapidly at the beginning of the summer and the fullest advantage is therefore taken of the short growing season.

The effect of climatic factors. The effect of temperature on growth in the arctic regions has received little detailed study. Despite the lower temperature optima which possibly characterize arctic plants there can be little doubt that temperature has an important influence on growth rates. Within any one region temperature changes are probably comparatively small and the wide variations in the type of vegetation found in different parts of any one region are to be explained mainly by reference to other factors. Comparatively little is known concerning the manner in which arctic plants are adapted for cold resistance; it is a subject which should repay detailed study. It may be noted here that plants of *Ranunculus glacialis* growing on Jan Mayen were not damaged when their leaves were cooled by a freezing mixture to −10° C. for about 1 hr.

The effects of the climate in determining the distribution of different types of vegetation on Jan Mayen have been examined in a previous paper (**20**). It has been shown that exposure to wind has a particularly marked effect and is perhaps the most important *climatic* factor controlling the differentiation of the various types of vegetation.

The effect of mineral nutrients. The extreme degree of nitrogen deficiency occurring over wide areas on Jan Mayen has already been examined in some detail (**19**). On the basis of these results it was concluded that nitrogen deficiency is widespread in arctic regions. In temperate regions the effects of nitrogen deficiency have been studied in considerable detail and it has been found that protein synthesis is greatly reduced, the rate of growth being consequently lowered (Gregory (**8**)).

Less information is at present available on the supply of other nutrients in the arctic, but since the effects of nitrogen deficiency mask other deficiency symptoms, the supply of phosphorus and potassium probably have a smaller effect on growth.

Other factors. In addition to the effects outlined above, ecological evidence shows that water supply and the time of the retreat of snow have a marked effect on the growth of plants (see (**20**)) in many of the localities studied.

The considerations brought forward in this discussion point to the conclusion that the growth of arctic plants is restricted as a result of low temperature, exposure to wind and, in the majority of situations, nitrogen deficiency; the photosynthetic mechanism appears on the other hand to be adequate for the requirements of the plants. For the further elucidation of these problems much detailed work is necessary, particularly in the direction of growth analysis, the examination of protein metabolism, and the comparative study of species of wide distribution in both temperate and arctic regions.

SUMMARY

1. Measurements of the assimilation rate were made and the level of sugars and starch determined, by analytical methods, in plant material collected on Jan Mayen Island.

2. The net assimilation rate of *Oxyria digyna* was found to be 0·30 gm. per sq. dm. per week towards the end of the growing season.

3. Considerable reserves of sugars and starch were present in the leaves and roots of *Oxyria digyna* and *Polygonum viviparum* as well as in the leaves of *Ranunculus glacialis.* Changes during the growing season and also the ratios between the various carbohydrate fractions were examined.

4. Significant diurnal changes in the starch and sugar levels were shown to take place in the leaves of *Oxyria digyna* during mid-August; the variation in the starch level being particularly marked.

5. Observations on the stomatal movements of *Oxyria digyna* and *Taraxacum croceum* showed that, although the stomata were continuously open, the aperture tended to be greater at the time of day when light intensity and temperature were highest.

6. The effect of the arctic environment on carbohydrate metabolism and growth is discussed.

7. It is concluded that, in the arctic, carbon assimilation proceeds at a rate sufficient to supply the requirements of growth and that the low growth rate of arctic plants is controlled by other factors; in this connexion the importance of exposure, temperature and nitrogen deficiency is emphasized.

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CHARCOALS FROM MAIDEN CASTLE AND THEIR SIGNIFICANCE IN RELATION TO THE VEGETATION AND CLIMATIC CONDITIONS IN PREHISTORIC TIMES

By E. J. SALISBURY and F. W. JANE

(*With four Figures in the Text*)

The material which forms the subject of this paper was placed in our hands for investigation by the late Mrs Mortimer Wheeler and Dr Mortimer Wheeler and was obtained during the recent excavations on the site of Maiden Castle. In addition we have included some data from charcoals obtained during the excavations on the Roman site at Verulamium. From the archaeological data the Dorset charcoals belong to three age groups, namely, Neolithic, Early Iron Age and Late Iron Age. These three levels correspond approximately to the periods of 2500–2000 B.C., 400–200 B.C. and 50 B.C.–A.D. 50. For the data upon which these figures are based the reader is referred to the reports upon the Maiden Castle excavations (*Antiq. J.* **15**, 237 (1935)).

THE NATURE OF THE MATERIAL

The general character of the material calls for some comment. Not only did the excavations provide a very large number of separate samples of charcoal, but in many of these it was possible to recognize fragments from a number of distinct stems so that the total number of specimens examined was exceptionally large. Indeed, so numerous were the specimens of hazel (*Corylus avellana*) and, in a lesser degree, of oak (*Quercus* sp.?) also, that it has been possible to obtain statistical data to which, as the sequel will show, some importance is attached.

The character of the specimens has considerable significance. Most of the charcoal stems are of comparatively small diameter and indeed, except for a few of the fragments of oak, were certainly in the nature of mere sticks or twigs. We can from this reasonably infer that the material was collected locally and probably in the immediate vicinity of the site, as it is evident that the sticks from which the charcoals are derived were often too small to have been worth carrying a distance. Had the wood been collected more than a short distance away it is reasonable to assume that the average diameter would have been larger and the proportion of very small twigs would have been small. If this contention be granted it follows that the charcoals are representatives of the vegetation of the chalk down itself and, as the identifications of the species will show, their nature is entirely consistent with this interpretation.

The second point of importance to be noted is that there is no evidence of selection, since, though there is a very marked preponderance of certain species, a sufficient number of others do occur to warrant the conclusion that this preponderance was an outcome of relative frequency and not of selection. That the charcoals represent a random sampling of the local vegetation is further indicated by the fact that there is evidence that the stems used for making the charcoal were not cut but were collections of dead sticks either picked up or broken off. This is not unlikely when we remember the rather inefficient tools available for felling and cutting. Inefficient in the sense that their keen edge would soon be blunted on hard wood and therefore they would naturally be reserved for more important work than that of obtaining fuel. As the senior author has elsewhere pointed out, there are grounds for thinking that primitive man was largely responsible for destroying the softer-wooded trees just because these were most easily felled with the implements at his disposal. The hazel and oak, which here preponderate, do not come within this category of soft-wooded easily felled trees. But the suggestion that the wood employed was dead wood rests on something more than mere supposition, for, in quite an appreciable number of instances, the charcoals contain bore-holes filled with carbonized "frass" which clearly marks the activities of beetle larvae of the type which attack dead and not living wood. Further, a few specimens of charcoal indicate by their texture that the wood was partially decayed before it became carbonized. It is then certain that some of the wood was dead when converted and this may well have been true of most if not all. A procedure so rational, at a period when, as already suggested, easily blunted implements would be reserved for purposes more important, may well have persisted long after the durability of the cutting edge of tools had been improved. One may well speculate as to whether the rights of obtaining dead wood "by hook or by crook", which persisted even in the jealously guarded areas under Forest Law, may not have been a privilege which survived even the restrictions due to the Norman passion for the chase, by reason of the fact that it was a custom going back to remote antiquity. Be this as it may, the fact that the charcoals probably represent collections of dead sticks renders it the more likely that they are a random sampling of the woody vegetation of the immediate vicinity in which the relative proportions may be taken as a rough approximation to the relative abundance of the different species. Adopting this view, though the proportion of tree twigs would perhaps be somewhat exaggerated, we are led to the very interesting conclusion that, since the great majority of the charcoals are either hazel or oak, the community was probably a more or less closed one and not an open scrub. For it is in closed or semi-closed plant communities that we find a predominance of one or few species, whereas in open scrub, such as that which we find occupying chalk downs to-day, there is a great variety of woody species, although two, namely, hawthorn (*Crataegus monogyna*) and hazel, may predominate.

Here at Maiden Castle, however, there is no evidence of hawthorn in the Neolithic and Early Iron Age periods, whilst the proportion of hazel is much higher than we should expect in open scrub. Further, the oak charcoal indicates the presence of oak trees which, when present in scrub, are a feature of the later phases of the plant succession when the scrub has become a closed community, rather than of the earlier phases when the scrub is still more or less open. We are thus led to picture the vegetation of the chalk down as clothed, not, as some have supposed, from the most remote past with grass, but in both Neolithic and Early Iron Age times, as consisting of woodland chiefly of hazel with occasional oak trees, not perhaps of any great size, and here and there scattered specimens of other species.

It is impossible to reconcile the nature and frequencies of the charcoals with any other mental picture of the vegetation. The apparent entire absence, at these earlier epochs, of some of the larger and commoner chalk-scrub shrubs, such as *Crataegus monogyna*, *Cornus sanguinea* and *Viburnum lantana*, is quite consistent with the picture we have presented, since they occur in the earlier more open phases of the scrub succession. On the other hand, the absence from our charcoals of damp habitat species and the prevalence of calcicoles does not admit of the supposition that the wood was collected at the foot of the downs rather than on the downs themselves.

To summarize, the evidence, though circumstantial, is nevertheless very definitely in favour of the view that the chalk downs were clothed, probably till Late Iron Age times, with more or less closed woodland of the oak-hazel type. This is the type of woodland that now predominates on the clay-with-flints which to-day covers the chalk in many areas. It is true that the downs near Maiden Castle have a very shallow soil overlying the chalk at the present time. But oaks will and do grow where the clay above the chalk is shallow, and it must not be overlooked that the forest destruction by primitive man at first, largely perhaps through the agency of fire, and subsequently, as his implements improved, by the use of his tools, not only destroyed the trees and shrubs but would certainly lead to considerable soil erosion so that the leached residue at the chalk surface, represented by the clay-with-flints, would be in large part removed by precipitation and washed down into the valley before the establishment of an efficient grass sward delayed or arrested the process. Conditions for woodland maintenance may therefore well have been formerly much more favourable than at the present time.

THE CONSTITUENT SPECIES

It may be emphasized that, once the necessary skill has been acquired in fracturing charcoals in the various planes with respect to the grain of the wood, the detailed structure can be ascertained with remarkable accuracy. Furthermore, in all critical instances we have carefully compared the prehistoric charcoals with samples of charcoal prepared from recent specimens, and by careful matching have been able to satisfy ourselves that the range of variation exhibited in the ancient charcoals of one type was comprised within the limits exhibited under modern conditions by the species to which we had attributed it.

In view of the use made in the sequel of the different "specimens" it may be well to emphasize what criteria have been employed for distinguishing charcoals regarded for our purposes as of separate origin. We have assumed that: (1) Charcoals from different locations or from different levels are from distinct specimens. For this the probability is very high that the assumption is valid. (2) That amongst the charcoals present in the same sample those which show the same rhythm in variation of the width of annual rings have been regarded as from the same specimen, whereas those showing a difference in rhythm have been regarded as distinct specimens. Here, too, we are probably not liable to appreciable error, but it must be recognized that different branches of the same bush or tree, perhaps owing to competition for food and water between the different branches, or owing to the fact that one branch is old and another young, resulting again in differences of water and food supply, may show differences in the annual ring rhythm of a smaller or larger degree. It is, however, very unlikely that such sources of error, if they occur, would appreciably affect the general conclusions based upon the entire collection. All we can say is that the real number of distinct individuals upon which our conclusions are based might be slightly fewer than appears, from the cause just mentioned, whilst their numbers may have been somewhat underestimated owing to branches of different trees or shrubs possessing the same rhythm of width of the annual increments of growth.

In Table 1 the complete list of woods identified is furnished for the different chronological periods together with an approximate estimate of the proportion of specimens of each species expressed as a percentage of the total number of specimens for the particular period.

Of the species listed in Table 1 all are typical of present-day woods on calcareous soil, and indeed the buckthorn (*Rhamnus catharticus*), the whitebeam (*Sorbus aria*) and the yew (*Taxus baccata*) are practically confined to soils of this type. The hazel is by far the most abundant of all the species present, being represented by about 140 distinct specimens (as defined above) in the Late Iron Age, and this preponderance is a feature of all three periods. The percentage of hazel in the Late Iron Age specimens is 50 % whilst in Neolithic times it is 40 %. The total number of charcoals from Early Iron Age levels is too few for any importance to attach to the exact proportions but the Hazel is the only species represented by more than a few "specimens".

It is not possible to distinguish the wood of *Quercus robur* from that of *Q. sessiliflora*, since we must concur in the statements of other authors that the woods of these two species are not histologically distinguishable. So we must content ourselves with saying that oak was the next most abundant type. Though the probability is that the specimens were of *Q. robur* the question must, in the absence of foliar material, be left open.

Table 1. *Identifications of charcoals from the different occupation levels at Maiden Castle, Dorset*

Species or genus	Neolithic level *ca.* 2500–2000 B.C.	Early Iron Age *ca.* 400–200 B.C.	Late Iron Age *ca.* 50 B.C.–A.D. 50
Acer ? campestre (maple)	—	Present	Present *ca.* 2·9%
Betula sp. (birch)	× × × × × × × ×	× × × × × × × ×	Present 1·5%
Corylus avellana (hazel)	Present *ca.* 40%	Present	Present *ca.* 50%
Crataegus sp. (hawthorn)	—	× × × × × × × ×	Present *ca.* 1·8%
Fraxinus excelsior (ash)	Present *ca.* 4%	× × × × × × ×	Present *ca.* 2·9%
Populus sp. (probably aspen)	Present *ca.* 1%	× × × × × × ×	× × × × × × × × × ×
Pyrus malus (apple)	Present *ca.* 16%	× × × × × × ×	Present *ca.* 1%
Quercus sp. (? *robur*) (oak)	Present *ca.* 23%	Present	Present *ca.* 35%
Rhamnus catharticus (buckthorn)	Present *ca.* 3%	× × × × × × × × ×	× × × × × × × × × ×
Salix sp. (willow)	Present	× × × × × × ×	Present *ca.* 1%
Sorbus aria (whitebeam)	Present	× × × × × × ×	× × × × × ×
Sorbus torminalis (service tree)	× × × × × ×	× × × × × × ×	Present
Taxus baccata (yew)	Present *ca.* 8%	Present	× × × × × × ×
Ulmus sp. (? *montana*) (wych ? elm)	× × × × × × ×	× × × × × × ×	Present *ca.* 1%
Prunus domestica (plum)	—	—	One plum stone
Prunus avium (cherry or gean)	—	—	Present *ca.* 1%
Prunus spinosa (blackthorn)	—	—	Present *ca.* 1·5%

Our material does not permit us to conclude whether the oak trees were large or small, since most of the specimens are obviously branches and large twigs and not main trunks. A few specimens were obviously fragments of main stems and suggested trees of perhaps slightly under rather than over the average size for the species.

The general character of the flora as shown by the specific composition and relative frequencies is only consistent with a closed community such as might be represented by an oak-hazel-coppice-with-standards at the present day, but with the difference that the hazel layer was not coppiced but probably grew as tall as in oak-hazel woods where the shrub layer is left uncut. In woods of this type the trees are normally infrequent and the associated shrubs few both in number of species and in number of individuals.

Of the trees which call for special mention the presence of the yew (*Taxus baccata*) in both the Early Iron Age and Neolithic levels is of particular interest from the point of view of geographical distribution and immigration. The view was at one time held that this tree was of recent growth in this country, and suggestions have even been made that it was a Roman introduction.. Clement Reid (1899), however, stated that the yew was common in Neolithic peat below sea-level in the Thames valley and the Fenland. The fact that it is, in our samples, represented by several specimens in the Early Iron Age and Neolithic charcoals and that also the nature of these precludes the possibility of their being fragments of implements imported from elsewhere, renders it certain that the yew was a native constituent of the vegetation of the western chalk in Neolithic times.

The absence of beech from the Neolithic charcoals may be accounted for not only by the fact that this tree was a late immigrant into Britain but also by the fact that even to-day there is some doubt as to whether the beech is native so far west (cf. Watt & Tansley, 1932). It would at least appear probable that this tree had not reached the Dorset chalk by the beginning of the first century A.D.

It is significant to note that the largest number of woody species are represented in the Neolithic charcoals despite the fact that the total number of distinct "specimens" for this period is only about half the number of those from the Late Iron Age levels. Thus the differences between the two periods are hardly likely, therefore, to be the outcome of mere errors of sampling.

If, as suggested, the trees were rather sparse, the differences in floristic composition might have been the outcome of selective destruction by man, but not only are the species absent from the later charcoals unlikely to have been removed for their utility, which is negligible, but also, with the exception of *Populus*, the other species represented in the Neolithic charcoals and not found in those from the later periods, namely, the buckthorn (*Rhamnus catharticus*) and the whitebeam (*Sorbus aria*), are both pronounced calcicoles. Furthermore, the yew, a tree practically confined to highly calcareous soils, is absent from the Late Iron Age charcoals and is represented by a single specimen only in the Early Iron Age charcoals, yet by no less than seven specimens in the Neolithic charcoals. We thus have a consistent suggestion of the diminution of the more calcicole types which is not controverted by the nature of the species which occur in the later and not in the earlier material. *Sorbus torminalis*, for instance, which is only present in the Late Iron Age charcoals, though it occurs on calcareous soils, is most frequent on soils that are more or less non-calcareous.

The erosion that would automatically follow destruction of the forest covering either by direct or indirect human agency would, at the outset, affect the soil on the steeper slopes which would probably be the last to be cleared. On the more level summits erosion would not take place until the oak and hazel had become at least sparse. Had this been the condition of the vegetation in Late Iron Age times we should have expected to have found the charcoals of more associated shrubs, but the floristic composition at that period suggests that the woody vegetation was then still not very open though the presence of hawthorn (*Crataegus* sp.), blackthorn (*Prunus spinosa*) and birch (*Betula* sp.), not found in the earlier samples, is indicative of a less closed community.

There is no reason to doubt that during the earlier part of the twenty to twenty-five centuries represented by our samples there would have been a steady augmentation of leached soil resulting in an ever-increasing thickness of clay, wherever the slope was not too great for its retention, the upper layers of which would become more and more depleted of their carbonates. Hence it is not improbable that the floristic changes indicated by our material were a direct outcome of edaphic changes which would continue until the destruction of the forest covering and with it the protective layer of humus, led to erosion and to gradual diminution of the clayey residue or even complete exposure of the unleached chalky subsoil. In this connexion we may note that the wych elm (*Ulmus montana*) and the cherry (*Prunus avium*) present in the Late Iron Age samples are both frequent constituents of oak-hazel (*Quercus robur-Corylus*) woods on calcareous clays to-day. Both are most frequently associated with shallow soil above the chalk. With the passage from a closed to an open community the exposure would increase, and thus conditions became less favourable to tree growth and this would be accentuated by the edaphic conditions as the diminished protection led to soil erosion.

EVIDENCE RESPECTING PAST CLIMATIC CONDITIONS

The unusual amount of material available from different levels of known age suggested that a unique opportunity was afforded for obtaining evidence regarding the climatic conditions of the past by means of the width of the annual rings.

The work of Douglas (1919) in America has established a clear correlation between rainfall and width of annual rings in the sequoias. He showed that certain rings exhibited marked resemblances over a wide stretch of country. Thus trees no less a distance than 750 miles apart showed a similar exceptionally narrow ring corresponding to the year 1850 (Douglas, 1920). The evidence is, in fact, conclusive that the width of the annual rings is markedly affected by the conditions of water supply, and that especially in the drier types of habitat the annual increment is mainly dependent upon the rainfall and humidity during the growing season. But, in assessing the utility of this climatic index, it must not be overlooked that other factors are involved, as, for instance, the density of the stands of trees and/or bushes.

The formation of multiple growth rings in a single season may sometimes occur when there is a definite check to activity, as may be caused by defoliation during the early part of the growing season which brings about a temporary diminution, or perhaps cessation, of cambial activity. In the material we have examined such partial growth rings were occasionally found in the specimens of oak charcoal and more rarely in those of hazel, but it should be emphasized that no difficulty was experienced in distinguishing between the annual increments themselves and such partial growth rings. It is, however, evident that stress must not be laid on individual specimens so much as on the general character of the annual increments in the samples of a particular period considered collectively and on the range of variation they exhibit in relation to those of the other periods and the charcoals of recent specimens.

It is therefore obvious that only where a number of specimens of the same species are available can the width of the annual rings be used as a criterion of the moisture conditions during the period of growth. Furthermore, as Douglass showed, the width of the annual rings during the period represented by the sequoias, namely, from about 1300 B.C., that is, 3200 years, show a periodicity approximating to that of the sunspot cycle of 11 years. Thus comparison of specimens of less than 11 years might reveal differences due to temporary rather than secular climatic changes. Again, crowded trees usually show narrow rings, whereas upon the same site, after thinning the newly formed rings of the trees that are left usually show a marked increase in width unless the increased exposure more than compensates for the diminished competition for water by the root systems. It is evident then that only where an appreciable number of specimens are available which are not contemporaneous can any reliance be placed on the width of rings as a climatic index unless the differences be of considerable magnitude. For this reason we have in the present instance confined our attention to the two species best represented, namely, hazel and oak.

The next point to establish is whether or not these species, in common with the sequoias, are sensitive to differences of rainfall. This has been ascertained by careful measurements of annual rings in recent specimens in relation to the rainfall of the years during which the respective rings were formed. Through the kindness of the Earl of Ilchester we have been able to examine a number of specimens of hazel grown on the chalk of Dorset, and in Fig. 1 the mean width of the annual rings of all the different specimens for corresponding years are plotted and also the rainfall for the months of the growing season in the same seasons. The correlation is so striking as to need no emphasis.

By converting a number of recent specimens of hazel stems into charcoal and measuring the width of the annual rings both before and after conversion, using various types of technique, such as slow and rapid combustion, it was possible to establish that the ratio of the width of the annual ring in the untreated wood to that after conversion was not significantly different whatever method was employed to produce the charcoal. So that, though we are not aware of the technique adopted by Neolithic or Iron Age Man to produce charcoal nor whether their techniques were the same, it would appear unlikely that any differences between their techniques and ours would introduce any source of error.

Having then established that the width of a ring in charcoal bears a definite relation to that in the original wood it is evident that to use the ring widths as climatic indices we must compare them with charcoals prepared from recent specimens. This we have done, employing for the purpose the specimens from the chalk of Dorset to which reference has already been made and also specimens from the chalk of other areas and from the clay-with-flints of Hertfordshire. For our purpose these have been treated as a random sampling of the ring widths of the present day whilst the ring widths of the charcoal specimens of the various periods represented in our archaeological material have likewise been regarded as random samplings of their respective periods.

A more probable source of error than those already mentioned is the fact that the annual increments vary in width with the age of the stem, the second annual increment being often appreciably wider than those formed subsequently. In Fig. 2 the average, minimum and maximum widths of hazel rings before and after conversion to charcoal are shown diagrammatically for a number of recent specimens, and it will be seen that whilst the general relation between the width of the ring in the wood and in the charcoal is maintained, the width of these increments varies markedly from year to year.

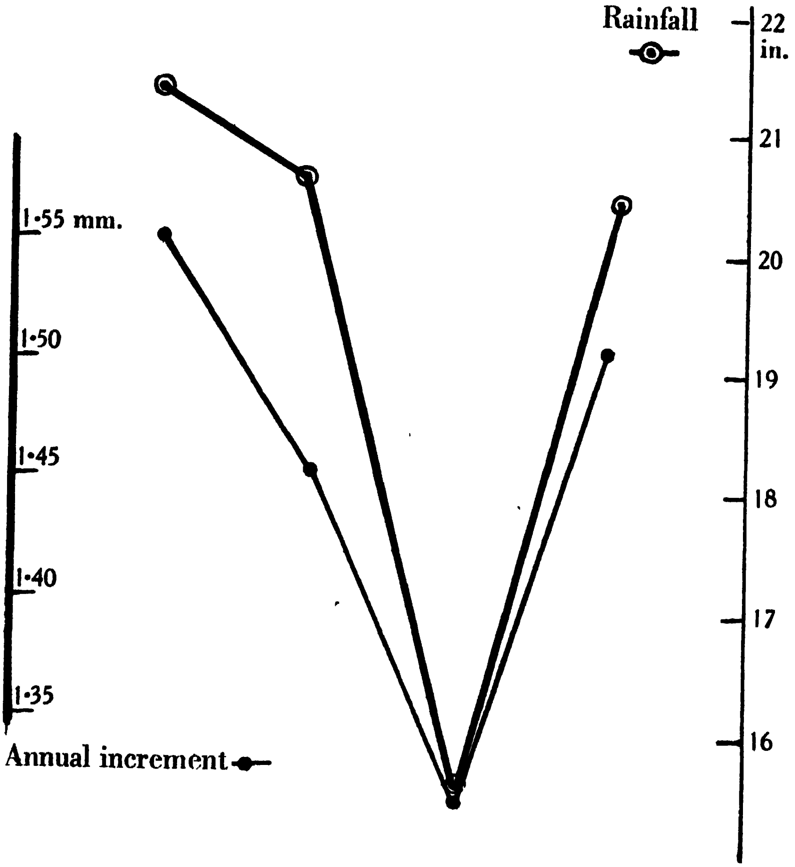

Fig. 1. The correlation between size of annual ring in hazel and the spring—summer rainfall.

In general the width of the first annual increment is subject to the greatest range of variation. The second annual increment, as already mentioned, is usually the widest, and the annual increments of the successive following years tend to show a steady diminution in width. This general trend of annual-increment width is shown when the climatic conditions are practically uniform and is mainly the outcome of the fact that the total annual volume increment under uniform conditions is similar, whereas the periphery is constantly augmenting so that a corresponding volume increment is necessarily accompanied by a diminished radial extension. To minimize this source of error very young specimens of charcoal of two or three years' growth have been omitted and specimens of recent charcoal for comparison with the prehistoric material have been obtained from stems of similar age.

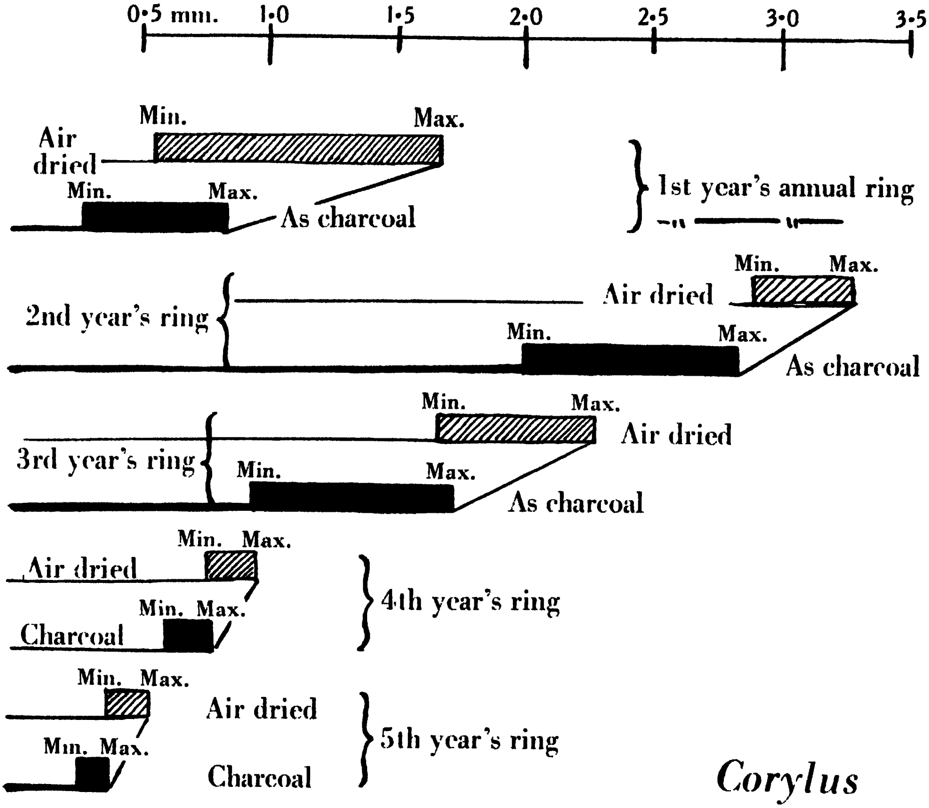

Fig. 2. Relation between annual ring diameter in fresh wood and charcoal (for explanation see text).

A total of 568 annual rings have been measured in recent charcoals of *Corylus avellana* whilst of Late Iron Age the number of rings measured is 578, of Early Iron Age 174 and of the Neolithic Period 186.

The actual measurements were made to the nearest 0·05 mm., and the data for the respective averages, for the standard deviations and for the standard errors of the means have been obtained from these figures. But as the class intervals are small and their number consequently large, having regard to the number of specimens, they have been grouped into half-millimetre categories in order to present graphically the trend of variation in a manner more readily apprehended (cf. Figs. 3, 4). In Table 2 the data for these half-millimetre class intervals are presented for each of the periods named, and to facilitate comparison the percentages to which they correspond are also furnished.

Table 2. *Width of annual rings of* Corylus avellana *in charcoals of specimens representing various epochs*

Width of annual increment	Recent specimens		Late Iron Age specimens		Early Iron Age specimens		Neolithic specimens	
mm.	No.	As %	No.	As %	No.	As %	No.	As %
Under 0·5	111	19·5	64	11·1	25	14·3	43	23·1
0·5–1·0	144	25·3	222	38·4	65	37·3	54	29·0
1·0–1·5	114	20·0	161	27·8	33	18·9	27	14·9
1·5–2·0	100	17·6	69	11·9	27	15·5	30	16·1
2·0–2·5	68	11·9	30	5·2	18	10·2	21	11·2
2·5–3·0	24	4·2	12	2·0	4	2·3	8	4·2
3·0–3·5	6	1·0	14	2·4	1	0·6	2	1·0
3·5–4·0	1	0·1	4	0·7	1	0·6	1	0·5
4·0–4·5	—	—	2	0·3	—	—	—	—
Totals	568		578		174		186	

The average values obtained for the charcoals of the various periods are remarkably close, as can be seen from Table 3 in which the mean values are furnished together with the standard deviations and the standard errors of the means.

Table 3. *Mean values for width of annual rings in* Corylus avellana *and their standard deviations*

	Neolithic specimens	Early Iron Age	Late Iron Age	Recent specimens
Mean width of annual increment (mm.)	1·1605	1·1825	1·1847	1·2376
Standard deviation	0·781	0·65395	0·69740	0·704
Standard error of mean	0·056	0·049	0·029	0·029

Although the differences between the mean values for the various periods are so small it is interesting to note that there is a very slight increase as we pass from the Neolithic charcoals to the Iron Age specimens and recent charcoals. This steady trend, if it have any significance, would seem to suggest that there was a tendency for the climatic conditions to become steadily more humid from Neolithic times to the present day. Actually, however, when we come to assess the differences between the means we find that in no instance is there a difference that is statistically significant. In Table 4 the differences are seen in most instances not to exceed their standard errors. In only two instances is this not the case, namely, for the differences between the means for the recent and Neolithic and the recent and Late Iron Age specimens. But as,

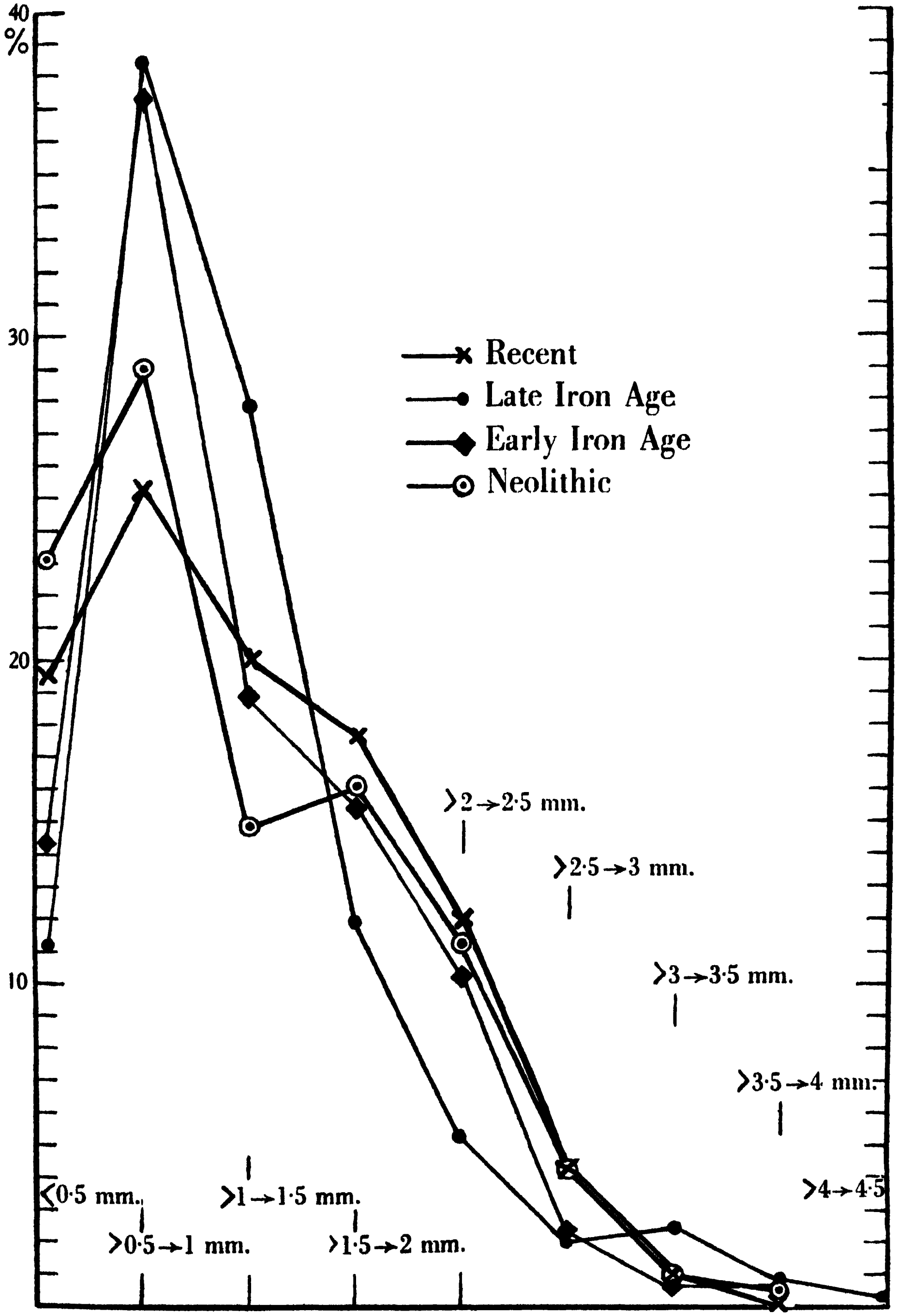

Fig. 3. Variation in width of annual ring of *Corylus avellana*.

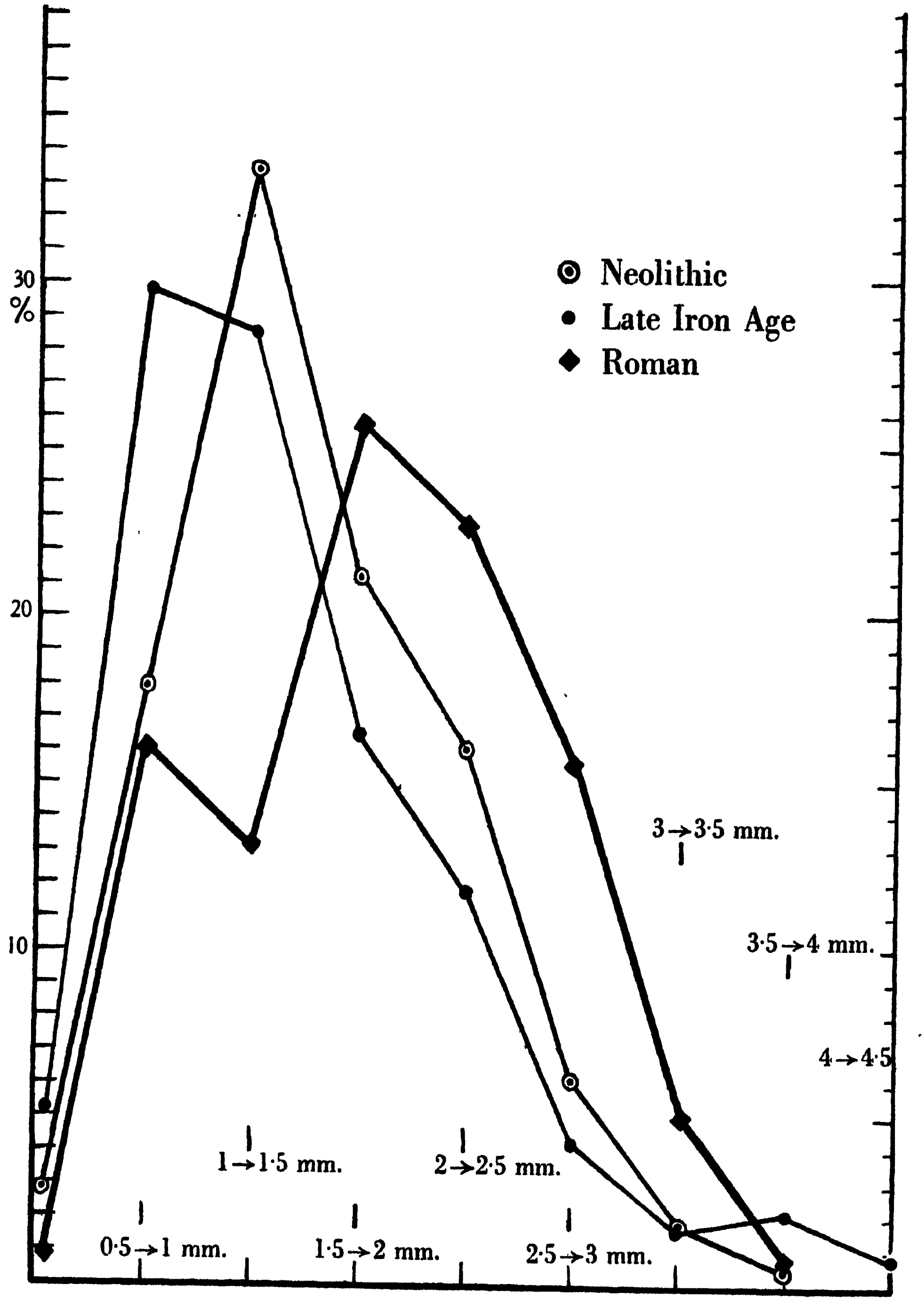

Fig. 4. Variation in width of annual ring of oak.

to have any probable significance, the difference should be at least three times its standard error we can safely assert that the data furnish no grounds for assuming any significant difference in the rate of growth of hazel during the past 4000 years.

Table 4. *Differences of means for widths of annual rings of* Corylus

	Difference	Standard error of difference	S.E.D. × 3
Recent—Neolithic	0·0771	0·063	0·189
Recent—Early Iron Age	0·0551	0·056	0·168
Recent—Late Iron Age	0·0529	0·041	0·123
Early Iron Age—Neolithic	0·0220	0·074	0·222
Late Iron Age—Neolithic	0·0242	0·063	0·189
Late Iron Age—Early Iron Age	0·0022	0·057	0·171

The graphic presentation of the data in Fig. 3 emphasizes the similarity in the variation curves for the different epochs. The general trend is essentially the same for all four periods with a mode between 0·5 and 1·0 mm. in each. Both Early and Late Iron Age material agree in exhibiting a rather higher percentage of rings approximating to the mode, a feature which is reflected in their lower standard deviations. On the other hand, the variation curves for the Recent and Neolithic charcoals exhibit throughout a remarkable degree of similarity, the proportions of rings in the higher class intervals being almost the same. These curves thus afford confirmation of the conclusions based on the average values.

QUERCUS

Although no other species affords such a number of annual rings as the hazel yet the number of specimens of oak is sufficient to warrant statistical treatment.

Compared with the hazel the oak has the disadvantage that the size of the specimens is much less uniform and hence it is far less easy to obtain recent material that can be regarded as strictly comparable with the prehistoric specimens. But despite this defect the material has considerable value as enabling us to ascertain in a second species whether the conclusions based upon the hazel are confirmed. To minimize the drawback already referred to only those prehistoric specimens have been included which were apparently portions of relatively small stems and similar material has been utilized for conversion to charcoal of recent oak. In addition to the material from Maiden Castle obtained from the same levels as the hazel material described above, we have utilized charcoals which were obtained during the Verulamium excavations and which belong to the Roman period. Although only a small sample of 136 rings they are nevertheless interesting for comparison.

Comparison of the average widths of the annual rings of the oak charcoals of the respective periods (Table 5) show a striking similarity between those of the Neolithic Period and of the Late Iron Age Period, the difference being

Table 5. *Width of annual rings in oak charcoals of different epochs*

Width of annual increment mm.	Neolithic		Early Iron Age		Late Iron Age		Roman	
	No.	%	No.	%	No.	%	No.	%
Under 0·5	6	2·8	—	—	28	5·1	1	0·7
0·5–1·0	38	17·9	12	40	163	29·8	22	16·1
1·0–1·5	71	33·4	7	23·3	156	28·5	18	13·2
1·5–2·0	45	21·2	5	16·6	90	16·4	35	25·7
2·0–2·5	34	16·0	1	3·3	64	11·7	31	22·7
2·5–3·0	13	6·1	3	10·0	21	3·9	21	15·6
3·0–3·5	4	1·8	2	6·6	9	1·6	7	5·1
3·5–4·0	1	0·4	—	—	11	2·0	1	0·7
4·0–4·5	—	—	—	—	4	0·7	—	—
4·5–5·0	—	—	—	—	1	0·2	—	—
Totals	212		30		547		136	
Average width of rings (mm.)	1·5345		1·468		1·447		1·87	
Standard deviation	0·614		0·791		0·780		0·71	
Standard error of mean	0·0451		0·126		0·0334		0·061	

0·0875 mm. and the standard error of this difference 0·05612. The difference is therefore not statistically significant. Despite the very small number of specimens of oak available from Early Iron Age levels yielding only thirty measurable annual rings the average width is almost the same as for the Neolithic specimens the difference being only 0·0665 mm. with a standard error of difference of 0·133. Although there is no significant difference between the annual increments for the Neolithic, Early Iron Age and Late Iron Age Periods (cf. Fig. 4), yet the mean values show a slight decrease from the oldest to the latest period. Though these differences are not "statistically significant", yet the slight diminution in the average width during the lapse of over two millennia, which these samples represent, may quite well have been the outcome of the increased exposure and perhaps also to erosion of the soil overlying the chalk which, as has already been suggested, may have taken place owing to the destruction of woodland through man's influence. At all events the changing composition of the species and their relative frequencies as represented in the charcoals of these three periods are quite consistent with the view that the soil conditions were becoming less favourable for the growth of the oak and if any importance is to be attached to these differences they are more probably to be attributed to change in local climatic and soil conditions than to any general climatic change.

It is indeed a striking fact that when we turn to the Roman oak charcoals derived from Verulamium situated not on a chalk soil and not on a ridge, but on heavy clay-with-flints located in the valley of the Ver, we find that the average width of the annual increments is appreciably greater than at these other epochs on the chalk and that the differences are moreover statistically significant (cf. Table 6).

Too few recent charcoals were obtained to permit of useful statistical comparison but they indicate a rather narrower annual increment.

Table 6. *Differences in width of mean annual increments in oak charcoals of various epochs*

Periods	Difference of means	Standard error of difference	S.E.D. × 3
Neolithic—Late Iron Age	0·0875	0·05612	0·16836
Roman—Neolithic	0·3355	0·0757	0·2271
Roman—Late Iron Age	0·423	0·063	0·189

SUMMARY

An account is given of the results of examination of a very large number of pieces of charcoal from Neolithic, Early Iron Age and Late Iron Age deposits from Maiden Castle probably representing several hundred individual trees and shrubs and comprising some seventeen species. From these specimens evidence is furnished that in Neolithic times the chalk of Dorset was probably clothed with a closed plant community of woodland of the oak-hazel type. As we pass from the earliest to the latest period there is evidence of change, probably due to continued climatic action resulting in leaching and a less calcicole flora whilst forest destruction by man led to a more open vegetation, less favourable edaphic conditions and ultimately no doubt to soil erosion.

Nearly two thousand annual increments of growth have been measured in the prehistoric charcoals of oak and hazel, and the results compared with measurements of annual rings in charcoals prepared from recent specimens of the same species. From a statistical analysis objective evidence is furnished indicating that the climatic conditions throughout the period represented were probably essentially similar to those obtaining at the present time.

The Early Iron Age specimens were few in number and included no species not present in the earlier or later periods. Species present in both Neolithic and Late Iron Age charcoals were: *Corylus avellana*, *Fraxinus excelsior*, *Pyrus malus*, *Quercus ? robur*, *Salix* sp. In the Neolithic charcoals only: *Populus* sp., *Rhamnus catharticus*, *Sorbus aria*. In both Neolithic and Early Iron Age: *Taxus baccata*. In Early and Late Iron Age: *Acer campestre*. In the Late Iron Age charcoals only: *Betula* sp., *Crataegus* sp., *Sorbus torminalis*, *Ulmus* sp., *Prunus domestica*, *P. avium*, and *P. spinosa*.

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THE EFFECT OF MANURING, GRAZING AND CUTTING ON THE YIELD, BOTANICAL AND CHEMICAL COMPOSITION OF NATURAL HILL PASTURES

I. YIELD AND BOTANICAL SECTION

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(*With Plates* 13–17)

Introduction

An experiment was commenced in April 1930 on the hill farms of Bwlchrosser and Llety-Ifan-hên, situated in north Cardiganshire, approximately 9–10 miles east of Aberystwyth. This experiment consisted in manuring the native hill herbage with artificial fertilizers and lime and grazing the herbage with sheep, both under a controlled system by means of fencing and under free-grazing conditions. The plots at Bwlchrosser were on a fescue-bent (*Agrostis*) sward, and were 850 ft. above sea-level. At Llety, one unit of plots was on a fescue-bent sward, and another on a *Molinia caerulea* sward, both units being at approximately 900 ft. The plots have received their amounts of fertilizers every spring since 1930, thus ten applications have been made in all up to the present date (autumn 1939). This fertilizing, together with the effect of the grazing, has resulted in very considerable changes in the botanical composition and productivity of the majority of the plots. These results up to and including the year 1937 have been previously published (**1**,**2**,**3**,**4**). The first of these papers dealt with the palatability aspect of the freely grazed unfenced plots, the second with four years' pasture yield data from the controlled fenced plots; the third and fourth publications with the botanical differences between the freely grazed and the controlled grazed plots.

Such marked changes in growth and composition had occurred by 1938 owing to the continually built-up fertility, and to the unexpected appearance of lowland species, that it was deemed advisable to withhold the grazings in the fenced plots during 1939 and to take periodic cuts of the herbage in order that the yields of the entire plots could be obtained. It was also important to investigate the obvious differences existing in the chemical composition between such widely contrasting herbage as the treatments had brought about. In 1939, therefore, chemical analyses of the cut herbage and of soil samples were undertaken in conjunction with the yield and botanical analyses.

THE ARRANGEMENT OF THE EXPERIMENT (E. 117)

The experiment consisted of five fenced and unfenced 1/100 acre plots at each centre. These plots were treated as follows:

(1) Lime at the rate of 2 tons per acre of calcium carbonate applied in 1930 and again in 1935 = plot Ca.

(2) Superphosphate at the rate of 4 cwt. per acre = plot P.

(3) Superphosphate as above, with the addition of kainit and sulphate of ammonia at 4 and 1 cwt. per acre respectively = plot PKN.

(4) As plot 3, but with the addition of lime at the above rate and time of application = plot CaPKN.

(5) A control plot, grazed, but not manured with the artificial fertilizers, or with lime.

The open series of plots was situated at a short distance from the fenced series at each centre, but they were not adjacent. In 1931 additional fenced CaPKN and control plots were added to each of the Llety centres to obtain hay and aftermath data.

The initial application of lime and manures was made in April 1930. The plots subsequently received each spring superphosphate, kainit and sulphate of ammonia in similar quantities to the above, while during the first four years of the trial when pasture yield data were obtained additional applications of sulphate of ammonia at ½ cwt. per acre were given to the PKN and CaPKN plots after each grazing. This additional quantity was discontinued from 1934 onwards.

The fenced plots were grazed monthly, the commencing date for each year being 1 May. Six grazings were made per season. For the first four years of the trial sheep were taken to the plots from the Welsh Plant Breeding Station, but subsequently the sheep of the hill farms have been used. The open series of plots have been freely grazed by the hill sheep, while at Bwlchrosser cattle as well as sheep have had access to the open plots. At Llety the grazing was altogether more heavy and concentrated on the fenced and controlled plots than on the open plots: at Bwlchrosser because the open area was smaller and because of the presence of cattle the controlled grazing was not much more intense than that on the open plots.

The technique adopted in 1939 was to take four cuts throughout the growing season. A botanical analysis of the herbage in each plot was made prior to each cut, using the percentage productivity estimation method. The herbage was cut with a scythe, and that growing in the corners of the plots with a hook. The herbage of the entire plot was then weighed and a 2 lb. sample of the fresh material taken for air-dry weight and chemical analysis. In order to obtain additional chemical evidence of the unimproved native herbage an extra control sample was taken at each cut by means of protecting a portion of the open hill herbage with a yard-square wire cage.

The dates at which cuts were taken in 1939 were as follows: 22 May, 14 July, 5 September and 30 October.

RESULTS

The contributions of each species to the herbage of the hill areas selected for investigation at the commencement of the trial in 1930 are given in Table 1 for the three centres. The analysis of the swards used for enclosed plots and open plots are given in each case. The scientific and common names of all species mentioned in this paper are given in an Appendix. It will be seen that the enclosed and open portions of the swards were not identical in composition at any of the centres, but that the herbage was of the same type. Thus at Bwlchrosser and at Llety-fescue (the fescue-bent sward at Llety-Ifan-hên) the open areas contained a greater proportion of bent (*Agrostis*) than existed in the enclosed areas, while at Llety-*Molinia* (the *Molinia caerulea* sward at Llety-Ifan-hên) the open area had rather more *Molinia* and *Nardus stricta* and less fescue than the enclosed area. Comparing the three centres it will be observed that while Bwlchrosser and Llety-fescue were sheep's fescue-*Agrostis* swards containing their usual associated grasses and miscellaneous herbs which with the two dominant grasses make up such swards, the Bwlchrosser pasture showed the important difference that it contained small amounts of wild white clover, smooth-stalked meadow grass and bird's foot trefoil. The initial presence of these species at Bwlchrosser affected the speed of improvement in the early years of the trial.

The herbage of the Llety-*Molinia* centre was, of course, entirely different from that of the other centres; *Molinia* contributed over two-thirds of the herbage, and although fescue and bent were present, the latter only amounted to a trace. The miscellaneous herb group of this centre differed chiefly in the greater proportion of heath-rush, bilberry and heather, and the presence of *Scirpus caespitosus*.

A brief summary of the earlier results

The yield data obtained in the first four years of the trial showed that grazing alone benefited the unmanured plots of the fescue-bent swards, but depleted the unmanured plots of the *Molinia* sward. Complete manuring gave the greatest increases in yield. The addition of calcium to nitrogen, phosphate and potash did not influence the yield of herbage, but phosphate and calcium applied singly had a marked effect upon yield. It was shown that the yield of these hill pastures could be considerably increased during the winter and early spring, and that complete manuring brought about a more uniform distribution of the yield over the season, particularly on the *Molinia* pasture. The statement hereunder gives the average annual yield over a three-year period for the plots at each centre. The hay plots are not directly comparable with the pasture plots as they were started a year later, but the

Table 1. *The percentage contribution of the species to the herbage of each centre at the commencement of the experiment in spring* 1930

Centre	Area	Fine-leaved fescue	Bent (*Agrostis* spp.)	*Molinia caerulea*	*Nardus stricta*	Heath grass	Sweet vernal	Yorkshire fog	Smooth-stalked meadow grass	Wild white clover	Bird's foot trefoil	Field woodrush	Tormentil	Heath bed-straw	*Carex* spp.	Heath rush	*Scirpus caespitosus*	Bilberry	Heather	Other herbs
Bwlchrosser	Enclosed	53	33	—	—	½	3½	T	1	T	½	1	4	½	1	—	—	T	—	2
	Open	48½	46	—	—	½	½	T	½	T	½	½	2½	T	½	—	—	T	—	T
Llety-fescue	Enclosed	65	20	T	1½	½	2½	—	—	—	—	3	4	1½	1½	T	—	T	½	T
	Open	59	31	4½	T	T	1	—	—	—	—	½	2	1	½	—	—	T	½	—
Llety-*Molinia*	Enclosed	17½	½	71	6	—	—	—	—	—	—	—	1	T	½	½	T	1½	1½	T
	Open	10½	T	72½	10	—	—	—	—	—	—	—	—	—	½	1½	2	2	1	—

T = trace. Other species = mouse-ear hawkweed, common speedwell, pignut and mountain pansy.

same number of harvest years have been averaged. The data are expressed in lb. per 1/100 acre of air-dry material.

	Bwlchrosser	Llety-fescue	Llety-*Molinia*
Pasture CaPKN	35·0	32·1	25·7
„ PKN	39·2	32·8	25·3
„ Ca	24·0	25·4	11·8
„ P	25·6	31·4	16·3
„ control	20·8	20·3	9·9
Hay CaPKN	—	34·8	27·0
„ control	—	17·0	7·8

Superphosphate had a very pronounced effect upon yield at the two Llety centres, compared with no manuring. The low yield of the control, or no manuring, plot at the *Molinia* centre, however, was caused by the *Molinia* being largely killed out by the grazing and its place not being completely colonized by the fescue and other species of the sward during this first period of the trial. This disappearance of the *Molinia* took place on the other plots of this centre, but the fertilizers so encouraged the fescue and bent, which formerly occupied small proportions of the sward, that they quickly spread and increased the productivity. This fact has been previously recorded by Davies & Jones (5) in earlier experiments at Llety when periodical cutting was the means of defoliation. The data of the present experiment show a greater relative yield from the CaPKN hay plots compared with the unmanured hay plots than is the case with the corresponding pasture plots. Usually the sum of hay and aftermath outyields the sum of a number of pasture cuts. The botanical composition of the fescue-bent swards was also influenced by the combination of grazing and fertilizing, as well as the *Molinia* sward mentioned above. The amounts of fescue decreased on the majority of the fertilized plots, and the amount of bent correspondingly increased. This was particularly the case on the PKN and CaPKN plots where also the yields of miscellaneous herbs decreased in proportion to the increase of the grasses.

The palatability data showed that marked differential grazing occurred among the fertilized plots. There was evidence that the fertilizers increased their respective ingredients in the chemical composition of the plants, and changes also took place in the botanical composition of the herbage. It was shown in fact that manures even with uncontrolled grazing can effect great improvement in all three types of hill pastures investigated, but especially in a *Molinia pasture.* Complete manuring, including lime, gave the best results in relative palatability and the effect of lime alone was greater than that of superphosphate alone. The initial absence of superior species in the swards at Llety did not prevent positive results being obtained.

With regard to the effects of the manurial and grazing treatments on the botanical composition of the fenced plots, compared with the open and therefore freely and selectively grazed plots, the annual analysis up to and including 1937 showed that the changes in the botanical composition of the plots had been continuous since the commencement of the experiment. In general the herbage in the fenced fescue-bent plots showed an increase of bent and a decrease of fescue under the influence of close periodical grazing. In the herbage of the open plots where this influence of regular and close grazing to the base did not occur the fescue was encouraged rather than the bent. The chief difference in the fenced and open *Molinia* plots was that there were greater proportions of *Molinia* in the herbage of all the open plots than in the corresponding fenced plots. The same difference in the type of grazing would account for this fact as for the fescue-bent relationship of the other centres. There developed correspondingly greater amounts of fescue and bent in the fenced *Molinia* plots compared with the open ones, and these species completely dominated the herbage of the CaPKN and PKN fenced plots after no less than two years of treatment. At Bwlchrosser smooth-stalked meadow grass increased to large amounts in the fenced CaPKN and PKN plots and, more particularly, in the fenced Ca plot which became dominated by this species. The open Ca plot, on the other hand, contained only 5 % of this grass and 25 % of miscellaneous species, chiefly *Carex* and ribgrass by 1937. Wild white clover also made a considerable difference in the plots at Bwlchrosser by increasing very rapidly in the open CaPKN and Ca plots, and later, in the P plot. One of the greatest changes in botanical composition which occurred in this trial was when lowland grasses and wild white clover voluntarily appeared in the plots at Llety, chiefly in the fenced plots. In 1934 Yorkshire fog appeared at both the Llety centres, with the addition of annual meadow grass at the *Molinia* centre. In 1935 rough- and smooth-stalked meadow grasses and wild white clover appeared in some of the fenced plots of the *Molinia* centre. In 1936 crested dogstail appeared at the same centre; wild white clover, rough-stalked meadow grass, timothy and cocksfoot appeared at the fescue centre. In 1937 tall fescue appeared in one plot of the same centre. Only a trace of any particular species was at first discernible, and it was noticeable that the treatments under which they were enabled to thrive were chiefly those of CaPKN and Ca. These volunteer lowland species caused a great economic improvement to occur in the fenced CaPKN plot of the *Molinia* centre. and later in the Ca plot of the same centre, and the CaPKN and Ca plots of the fescue centre. The earliest and most marked change, however, took place in the fenced and intensively grazed CaPKN plot of the *Molinia* centre. At the commencement of the trial, in 1930, there was over 70% *Molinia* in the herbage, but by 1934 this plot consisted almost entirely of fescue and bent. By 1937 these two grasses together only amounted to 5 % of the herbage, while volunteer lowland grasses and wild white clover accounted for 92 %. Further reference to this factor of the entrance and spread of these volunteer species will be made when the data of the later years are discussed. It may be well to add here, however, that these species also appeared at Bwlchrosser, rough-stalked meadow grass appearing in 1936 and other species in later years. As previously stated, smooth-stalked meadow grass and wild white clover were initially present in small amounts at this centre.

Present (1938–1939) *results*

I. *The enclosed plots:* (*a*) *botanical changes.* The changes in the botanical composition of the enclosed and heavily grazed plots became increasingly rapid from 1937 onwards, particularly at the Llety centres, owing to the vigorous colonization of the volunteer grasses and wild white clover which had already gained a foothold. The botanical analysis for the plots at each centre in respect of the chief species are given in Table 2 for the years 1937 and 1938, the data for 1937 being reproduced from a previous report (4) for the purpose of comparison.

The Bwlchrosser data show that although the herbage at this centre was originally composed chiefly of fescue and bent, as depicted in Table 1, by 1938 only the control plot remained in this category. The growth of smooth- and rough-stalked meadow grasses had altered the composition of the fertilized plots. It will be seen that rough-stalked meadow grass made a very rapid increase under all manurial treatments in the period 1937–8. At the Llety-fescue centre the chief changes in the enclosed plots were again a marked increase in the proportions of rough-stalked meadow grass and wild white clover. The PKN and control plots were still devoid of these species. Fescue had increased in all the plots, with the exception of Ca, after several years of suppression in the manured plots by bent, but the PKN plot was still chiefly a bent plot. At the Llety-*Molinia* centre the colonization by lowland species was almost complete in the CaPKN plot by 1938, and they amounted to 96% of the herbage. The *Molinia*, as shown in Table 1, which originally formed 71% of the herbage had disappeared from all the pasture plots by 1938, with the exception of the Control. Fine-leaved fescue decreased to still lower proportions in the completely manured plots, but increased in the P plot. The Ca plot retained the mixed herbage that it had gradually acquired, and its proportion of white clover had increased by 1938. Yorkshire fog had increased rapidly in the CaPKN and PKN plots.

In general, the botanical composition of the enclosed pasture plots at all three centres was changing from a composition of hill species to a mixture of hill and lowland species, and even in some instances to an almost entirely lowland herbage. This change was most rapid from 1937 onwards. The growth of lowland species gave a patchy appearance to the herbage, for they occurred among the native species as colonies on account of each having been derived in most instances from a single plant. The hay with aftermath plots changed very little with respect to volunteer species, as will be seen when the yields are discussed.

(*b*) *Aggregate yields.* The yields from each plot in 1939 are given in Table 3 in terms of the aggregate yield from the four cuts during the growing season. In order to give a direct comparison the hay-aftermath plots were on this occasion cut four times in a manner similar to the pasture plots. The weights

Table 2. *The composition of the enclosed plots at Bwlchrosser, Llety-fescue, and Llety-*Molinia *in* 1937 *and* 1938 *based on a percentage tiller estimation*

		Bwlchrosser							Llety-fescue						Llety-*Molinia*								
Plot	Year	Fine leaved fescue	Bent (*Agrostis* spp.)	Yorkshire fog	Smooth-stalked meadow grass	Rough-stalked meadow grass	Wild white clover	Other spp.	Fine leaved fescue	Bent (*Agrostis* spp.)	Yorkshire fog	Rough-stalked meadow grass	Wild white clover	Other spp.	*Molinia caerulea*	Fine leaved fescue	Bent (*Agrostis* spp.)	Yorkshire fog	Smooth-stalked meadow grass	Rough-stalked meadow grass	Annual meadow grass	Wild white clover	Other spp.
CaPKN	1937	53½	9	3½	27	6½	½	T	4	79½	1	15	½	T	1	2½	2½	13	—	66	3	10	2
	1938	28	9½	T	31½	28½	2	½	21	35	1½	30½	12	T	—	T	4	35	—	43	7	11	T
PKN	1937	23	52½	4	16	4½	—	T	2½	88½	9	—	—	T	—	7	85½	4	—	—	3½	—	T
	1938	20½	39	5	20	15½	—	T	7	82	11	—	—	T	—	1	68	22	—	3	6	—	T
Ca	1937	15½	12½	3	63	1	1	4	52	40	—	2½	1½	4	2	54½	3½	4½	15	12½	—	4½	3½
	1938	15½	T	4½	60	17½	1½	1	44	40	—	10	4	2	—	52	½	3	12	15	3	7	7½
P	1937	50	35	2	—	2	1	10	12½	84	2½	—	—	1	T	34	66	—	—	—	—	—	T
	1938	26½	38½	8	—	22½	1½	3	38	52	2½	6	½	1	—	56½	38	2	—	½	1	—	2
Control	1937	52½	38½	—	—	—	T	9	48½	47	—	—	—	4½	4½	84	6½	—	—	—	—	—	5
	1938	65	31½	T	T	—	T	3½	51½	45	—	—	—	3½	4	73½	18	—	—	—	—	—	4½

Other species = sweet vernal, heath grass (*Triodia decumbens*), *Nardus stricta*, field woodrush, tormentil, heath bedstraw, bilberry, *Carex* spp., heath rush (*Juncus squarrosus*), sheep's sorrel, yarrow and ribgrass.

are expressed in pounds of air-dry material per 1/100 acre, and in tons per acre. The yields relative to the pasture control plot at 100 for each individual centre are also given.

It will be observed that of the pasture plots CaPKN gave the heaviest yield of air-dry material at each of the three centres, and that the remaining plots gave decreasing yields in the same order, namely, PKN, Ca, P and control. There were only small differences, however, between the Ca and P plots at Bwlchrosser, and between the PKN and Ca plots of the Llety-fescue centre. The differences in the yields of the Llety-*Molinia* plots were wider and more regularly spaced than at the other centres. Here the improvement of the fertilized plots over the control was more marked with the exception of the P plot. PKN and Ca plots gave greater yields than at Llety-fescue or Bwlchrosser, and in view of the low yield of the control plot their relative yields and those of the CaPKN plot at this *Molinia* centre were considerably higher.

Table 3. *The aggregate yields from the enclosed plots at each centre during* 1939 *in lb. per* 1/100 *acre, and in tons per acre of air-dry material; also the yields relative to the pasture controls at* 100

	Bwlchrosser			Llety-fescue			Llety-*Molinia*		
Plot	lb. per 1/100 acre	Tons per acre	Relative	lb. per 1/100 acre	Tons per acre	Relative	lb. per 1/100 acre	Tons per acre	Relative
Pasture CaPKN	72·21	3·22	474	77·02	3·44	415	77·36	3·45	640
„ PKN	56·44	2·52	371	53·17	2·37	286	62·69	2·80	518
„ Ca	46·86	2·09	308	52·28	2·33	281	55·48	2·47	458
„ P	45·13	2·01	296	48·47	2·16	260	33·06	1·48	274
„ Control	15·13	0·68	100	18·50	0·83	100	12·01	0·54	100
Hay CaPKN	—	—	—	40·48	1·81	218	13·71	0·61	113
„ Control	—	—	—	16·14	0·72	87	8·08	0·36	67

The hay plots which, as previously indicated, were cut at the same dates in 1939 as the pasture plots gave much lower yields at each centre than the CaPKN and control plots under pasture conditions. At the fescue centre the CaPKN hay plot gave a considerably lower yield than the P pasture plot, while at the *Molinia* centre this manurial treatment gave only a slightly better yield than the pasture control plot. This remarkable influence of a combination of intensive grazing (with consequent urination and dunging) and artificial manuring is perhaps seen more clearly if reference is made to the relative figures in Table 3, where it will be observed that the CaPKN hay yield at the fescue centre was 218 relative to the pasture control at 100, and that the CaPKN pasture yield was 415. The corresponding figures at the *Molinia* centre were 113 for the hay and 640 for the pasture.

Comparing the actual yields of centre with centre, the CaPKN pasture plots of Llety-fescue and Llety-*Molinia* gave the greatest yields and they were almost identical. They were, however, not greatly in excess of the CaPKN yield at Bwlchrosser. The PKN and Ca plots at the *Molinia* centre gave greater yields than at the other centres, but the position was reversed for the P and control plots. The CaPKN hay plot of the Llety-fescue centre gave nearly three times the yield of the same treatment at the *Molinia* centre, while the fescue hay control gave double the yield of the *Molinia* hay control. The reason for this disparity of the pasture P and control yields and the hay CaPKN and control yields at the *Molinia* centre, compared with their counterparts at the fescue centre, will be made apparent when their botanical composition is discussed.

(*c*) *Yields of individual species.* Yields in pounds per 1/100 acre of air-dry material of each species composing the herbage of the plots at the four cuts in 1939 are given in Tables 4–6. As has already been mentioned in the section dealing with previous results, the volunteer entry of certain lowland species into these hill plots proved a vital factor in their ultimate composition. An extraction of the data on these species in the above tables has been made, and is given in Table 7 in the form of a percentage contribution of native grasses, volunteer grasses, volunteer wild white clover and miscellaneous herbs to the aggregate season's yield for each plot. Reference will be made to this table when discussing the details for each centre.

The yields of individual species at Bwlchrosser are given in Table 4. With regard to the volunteer species at this centre, it will be remembered that there were very small amounts of Yorkshire fog, smooth-stalked meadow grass and wild white clover in the original sward at this centre, whereas these species, with the addition of rough-stalked meadow grass, only appeared at the Llety centres some years after the commencement of the trial. With reference to the grouping of the species it has been felt that a better comparison among the centres is obtained by considering the contributions of the above species as volunteer in each case.

The data in Table 4 show that fine-leaved fescue contributed most of any single species to the aggregate season's yield of the Bwlchrosser CaPKN plot. In the herbage of this particular plot red fescue was more abundant than sheep's fescue. Bent gave less than one-third of the fescue yield, and was exceeded by both the meadow grasses and wild white clover. Reference to Table 7 shows that approximately 50% of the aggregate yield consisted of lowland grasses and white clover. The herbage of the PKN plot differed from the CaPKN by having bent as the chief contributor. The yield of fescue was over half that of bent, but was not greatly in excess of the two meadow grasses. The most important difference, however, was that there was only a trace of clover in the PKN herbage. The Ca plot had, as seen in Table 7, the greatest percentage of lowland grasses in its yield, which together with the wild white clover contributed nearly 70% of the herbage. The actual yields of rough-stalked meadow grass and white clover for the season, however, were less than the yields of these species in the CaPKN plot. There were greater amounts of miscellaneous herbs in the Ca herbage than in the herbage of the other treatments. The P plot resembled the CaPKN in having fescue as the chief contributor. Bent was second

Table 4. *The yield in lb. per* 1/100 *acre of air-dry material of each species at the Bwlchrosser centre for each cut in* 1939

		Native species				Volunteer species*					Native and volunteer herbs							
Plot	Cut	Fine-leaved fescue	Bent (*Agrostis* spp.)	Heath grass	Sweet vernal	Yorkshire fog	Smooth-stalked meadow grass	Rough-stalked meadow grass	Other grasses	Wild white clover	Field woodrush	Tormentil	Heath bed-straw	*Carex* spp.	Yarrow	Sheep's sorrel	Other herbs	Total yields
CaPKN	1	7·82	0·87	—	—	T	2·61	5·40	—	0·70	T	—	—	—	—	—	—	17·40
	2	7·04	3·31	—	—	1·04	2·07	5·17	T	2·07	T	—	—	—	—	—	—	20·70
	3	5·13	3·24	—	—	0·90	1·80	1·80	T	5·13	T	—	—	—	—	—	—	18·00
	4	7·72	0·81	—	—	0·32	2·42	1·61	0·81	2·42	T	—	—	—	—	—	—	16·11
	Aggregate	27·71	8·23	—	—	2·26	8·90	13·98	0·81	10·32	T	—	—	—	—	—	—	72·21
PKN	1	3·23	1·97	—	—	0·16	1·18	1·34	—	T	—	—	—	—	—	—	T	7·88
	2	4·94	8·60	—	—	1·23	3·68	6·15	T	T	—	—	—	—	—	—	T	24·60
	3	3·08	6·54	—	—	1·16	3·08	1·54	T	T	—	—	—	—	—	—	T	15·40
	4	1·28	3·00	—	—	0·43	3·42	0·43	T	T	—	—	—	—	—	—	T	8·56
	Aggregate	12·53	20·11	—	—	2·98	11·36	9·46	T	T	—	—	—	—	—	—	T	56·44
Ca	1	1·15	0·17	—	—	T	1·44	2·41	T	0·35	0·12	—	—	—	0·06	0·06	T	5·76
	2	2·27	3·78	—	—	2·27	1·52	3·79	T	1·52	T	—	—	—	T	T	T	15·15
	3	3·16	1·26	—	—	0·79	3·95	1·90	T	3·95	T	—	—	—	T	0·79	T	15·80
	4	2·03	0·51	—	—	1·02	3·04	2·53	T	1·02	T	—	—	—	T	T	T	10·15
	Aggregate	8·61	5·72	—	—	4·08	9·95	10·63	T	6·84	0·12	—	—	—	0·06	0·85	T	46·86
P	1	2·99	1·12	—	0·22	T	0·37	1·79	—	0·52	0·30	—	—	—	T	—	0·15	7·46
	2	4·53	4·53	—	0·30	0·76	0·45	1·51	—	3·02	T	—	—	—	T	—	T	15·10
	3	4·78	2·39	—	T	0·28	0·28	1·41	—	4·91	T	—	—	—	T	—	T	14·05
	4	3·23	3·15	—	T	T	0·43	0·43	—	1·28	T	—	—	—	T	—	T	8·52
	Aggregate	15·53	11·19	—	0·52	1·04	1·53	5·14	—	9·73	0·30	—	—	—	T	—	0·15	45·13
Control	1	0·50	0·31	0·02	0·06	—	0·05	0·02	—	T	0·04	0·03	0·01	—	T	—	T	1·04
	2	2·10	2·27	0·26	0·26	T	0·11	T	T	T	T	0·26	T	—	T	—	T	5·26
	3	1·56	1·03	0·15	0·09	T	0·06	0·03	T	T	T	T	T	—	T	—	0·03	2·95
	4	2·76	2·59	0·12	0·06	T	0·06	T	T	T	T	0·29	T	—	T	—	T	5·88
	Aggregate	6·92	6·20	0·55	0·47	T	0·28	0·05	T	T	0·04	0·58	0·01	—	T	—	0·03	15·13
Cage (%)	1	46	27	13	2	—	—	—	—	—	1	3	1	T	5	—	2	100
	2	45	20	10	5	—	—	—	—	—	T	10	T	5	5	—	T	100
	3	40	28	5	5	—	—	—	—	—	T	10	5	2	5	—	T	100
	4	43	33	5	10	—	—	—	—	—	T	5	T	2	2	—	T	100

Other grasses = Perennial rye-grass, cocksfoot and timothy.
Other herbs = Mouse-ear chickweed, dandelion, hawkbit, ribgrass, buttercup, mouse-ear hawkweed, mountain pansy and pignut.
* See comment under "Yield of individual species".

Table 5. *The yield in lb. per 1/100 acre of air-dry material of each species at the Llety-fescue centre for each cut in* 1939

		Native species				Volunteer species					Native and volunteer herbs					
Plot	Cut	Fine-leaved fescue	Bent (*Agrostis* spp.)	Heath grass	Sweet vernal	Yorkshire fog	Smooth-stalked meadow grass	Rough-stalked meadow grass	Other grasses	Wild white clover	Field wood-rush	Tormentil	Heath bed-straw	Yarrow	Other herbs	Total yield
CaPKN	1	0·38	6·50	—	—	T	0·58	9·94	T	1·72	T	—	—	—	T	19·12
	2	T	8·91	—	—	T	2·97	8·91	T	8·91	T	—	—	—	T	29·70
	3	T	4·80	—	—	T	1·92	3·84	T	8·64	T	—	—	—	T	19·20
	4	T	4·50	—	—	T	0·90	1·80	T	1·80	T	—	—	—	T	9·00
	Aggregate	0·38	24·71	—	—	T	6·37	24·49	T	21·07	T	—	—	—	T	77·02
PKN	1	0·03	4·70	—	0·03	T	—	T	T	—	T	T	—	—	T	4·76
	2	T	20·34	—	T	1·07	—	T	T	—	T	T	—	—	T	21·41
	3	T	20·80	—	T	1·10	—	T	T	—	T	T	—	—	T	21·90
	4	T	4·84	—	T	0·26	—	T	T	—	T	T	—	—	T	5·10
	Aggregate	0·03	50·68	—	0·03	2·43	—	T	T	—	T	T	—	—	T	53·17
Ca	1	2·05	2·05	—	0·07	0·07	0·22	1·47	T	0·88	0·15	T	T	0·37	T	7·33
	2	3·71	4·33	—	T	T	0·47	1·55	0·78	3·88	T	T	T	0·78	T	15·50
	3	4·85	6·45	—	T	T	0·95	0·76	0·76	3·80	T	T	T	1·43	T	19·00
	4	1·57	5·42	—	T	T	0·42	0·42	T	1·57	T	T	T	1·05	T	10·45
	Aggregate	12·18	18·25	—	0·07	0·07	2·06	4·20	1·54	10·13	0·15	T	T	3·63	T	52·28
P	1	0·77	4·55	—	—	T	—	0·64	T	0·19	0·16	—	—	0·06	T	6·37
	2	0·56	13·68	—	—	T	—	1·88	0·94	0·75	T	—	—	0·94	T	18·75
	3	0·34	13·39	T	T	T	—	0·50	0·34	0·83	T	—	—	1·25	T	16·65
	4	0·13	5·69	0·07	T	T	—	0·13	0·13	0·35	T	—	—	0·20	T	6·70
	Aggregate	1·80	37·31	0·07	T	T	—	3·15	1·41	2·12	0·16	—	—	2·45	T	48·47
Control	1	0·74	0·26	0·06	0·04	—	—	—	—	—	0·04	0·01	0·01	0·02	T	1·18
	2	1·99	2·08	0·15	0·25	—	—	—	—	—	T	T	0·25	0·25	T	4·97
	3	3·04	2·76	0·36	0·36	—	—	—	—	—	T	0·36	0·22	0·15	T	7·25
	4	1·99	2·39	0·26	0·10	—	—	—	—	—	T	0·10	0·26	T	T	5·10
	Aggregate	7·76	7·49	0·83	0·75	—	—	—	—	—	0·04	0·47	0·74	0·42	T	18·50
Hay CaPKN	1	5·39	1·74	—	—	—	—	—	0·57	—	0·96	—	—	0·05	T	8·71
	2	5·94	6·98	—	T	—	—	—	1·56	—	0·30	—	—	0·08	T	14·86
	3	3·74	2·99	—	T	—	—	—	0·54	—	0·08	—	—	0·31	T	7·66
	4	4·81	3·97	—	T	T	—	—	0·19	—	0·09	—	—	0·19	T	9·25
	Aggregate	19·88	15·68	—	T	T	—	—	2·86	—	1·43	—	—	0·63	T	40·48
Hay control	1	2·32	0·45	0·06	—	—	—	—	—	—	0·09	0·03	0·02	—	T	2·97
	2	1·97	1·38	0·39	—	—	—	—	—	—	0·20	T	T	—	T	3·94
	3	2·68	1·72	0·51	—	—	—	—	—	—	0·10	T	0·05	—	T	5·06
	4	1·87	1·67	0·21	—	—	—	—	—	—	0·21	T	0·21	—	T	4·17
	Aggregate	8·84	5·22	1·17	—	—	—	—	—	—	0·60	0·03	0·28	—	T	16·14
Cage (%)	1	69½	24	½	—	—	—	—	—	—	2	4	T	—	T	100
	2	64	20	1	—	—	—	—	—	—	5	5	T	—	5	100
	3	45	25	5	—	—	—	—	—	—	15	5	5	—	T	100
	4	48	35	2	—	—	—	—	—	—	5	5	5	—	T	100

Other grasses = *Aira flexuosa*, *Nardus stricta*, annual meadow grass, perennial rye-grass, cocksfoot, timothy, crested dogstail, meadow foxtail.
Other herbs = mountain pansy, *Carex* spp. mouse-ear chickweed, dandelion, sheep's sorrel, broad-leaved plantain, harebell and red clover.

Table 6. *The yield in lb. per* 1/100 *acre of air-dry material of each species at the Llety-*Molinia *centre for each cut in* 1939

		Native species						Volunteer species						Native and volunteer herbs				
Plot	Cut	*Molinia caerulea*	Fine-leaved fescue	Bent (*Agrostis* spp.)	*Nardus stricta*	Heath grass	Sweet vernal	Yorkshire fog	Smooth-stalked meadow grass	Rough-stalked meadow grass	Annual meadow grass	Other grasses	Wild white clover	*Carex* spp.	Bilberry	Heather	Other herbs	Total yields
CaPKN	1	—	0·54	0·40	—	—	—	T	—	10·31	0·54	T	1·61	—	—	—	—	13·40
	2	—	0·25	0·25	—	—	—	1·23	—	10·60	1·23	T	11·09	—	—	—	T	24·65
	3	—	T	0·29	—	—	—	4·42	—	8·52	1·47	T	14·70	—	—	—	T	29·40
	4	—	T	0·50	—	—	—	1·49	—	4·25	0·20	T	3·47	—	—	—	T	9·91
	Aggregate	—	0·79	1·44	—	—	—	7·14	—	33·68	3·44	T	30·87	—	—	—	T	77·36
PKN	1	—	T	7·15	—	—	—	0·17	—	0·78	0·44	0·17	—	—	—	—	—	8·71
	2	—	T	17·32	—	—	—	10·38	—	3·47	3·47	T	—	—	—	—	—	34·64
	3	—	T	6·03	—	—	—	4·03	—	0·58	0·86	T	—	—	—	—	—	11·50
	4	—	T	6·11	—	—	—	1·18	—	0·16	0·39	T	—	—	—	—	—	7·84
	Aggregate	—	T	36·61	—	—	—	15·76	—	4·99	5·16	0·17	—	—	—	—	—	62·69
Ca	1	—	1·68	0·69	0·10	—	T	T	1·33	2·97	0·20	T	2·47	—	—	—	0·44	9·88
	2	—	1·02	0·82	T	—	T	1·02	2·04	4·08	T	T	11·22	—	—	—	0·20	20·40
	3	—	1·08	0·68	T	—	T	1·08	1·35	1·08	0·14	T	8·09	—	—	—	T	13·50
	4	—	1·17	0·59	T	—	T	1·17	2·92	1·76	0·59	T	3·50	—	—	—	T	11·70
	Aggregate	—	4·95	2·78	0·10	—	T	3·27	7·64	9·89	0·93	T	25·28	—	—	—	0·64	55·48
P	1	T	0·29	1·97	T	—	0·32	0·03	—	0·23	0·06	T	—	0·03	—	—	T	2·93
	2	T	0·71	10·56	T	—	0·71	0·71	—	1·41	T	T	—	T	—	—	T	14·10
	3	T	2·42	5·15	T	—	0·46	0·64	—	0·46	T	T	—	T	—	—	T	9·13
	4	T	3·86	2·07	T	—	0·14	0·69	—	0·14	T	T	—	T	—	—	T	6·90
	Aggregate	T	7·28	19·75	T	—	1·63	2·07	—	2·24	0·06	T	—	0·03	—	—	T	33·06
Control	1	0·20	0·92	0·04	0·03	0·05	—	—	—	—	—	—	—	0·09	0·02	T	T	1·35
	2	0·91	0·78	0·41	0·41	0·03	—	—	—	—	—	—	—	0·14	T	0·03	T	2·71
	3	0·37	1·07	0·14	0·21	0·06	—	T	—	—	—	—	—	0·10	T	0·10	T	2·05
	4	1·48	2·11	0·59	0·89	0·59	—	T	—	—	—	—	—	0·12	T	0·12	T	5·90
	Aggregate	2·96	4·88	1·18	1·54	0·73	—	T	—	—	—	—	—	0·45	0·02	0·25	T	12·01
Hay CaPKN	1	0·11	2·56	0·17	T	—	—	—	—	—	—	—	—	T	—	—	T	2·84
	2	0·62	5·30	0·31	T	—	—	T	—	—	—	—	—	T	—	—	T	6·23
	3	0·09	1·54	0·09	T	—	—	T	—	—	—	—	—	T	—	—	T	1·72
	4	0·15	2·68	0·09	T	—	—	T	—	—	—	—	—	T	—	—	T	2·92
	Aggregate	0·97	12·08	0·66	T	—	-	T	—	—	—	—	—	T	—	—	T	13·71
Hay control	1	0·21	0·30	T	0·02	—	—	—	—	—	—	—	—	0·01	0·02	0·06	T	0·62
	2	1·08	0·92	T	0·47	—	—	—	—	—	—	—	—	T	0·16	0·47	T	3·10
	3	0·29	0·24	T	0·09	—	—	—	—	—	—	—	—	T	0·02	0·29	T	0·93
	4	1·03	0·86	T	0·34	—	—	—	—	—	—	—	—	T	0·34	0·86	T	3·43
	Aggregate	2·61	2·32	T	0·92	—	—	—	—	—	—	—	—	0·01	0·54	1·68	T	8·08
Cage (%)	1	40	48½	T	4	—	—	—	—	—	—	—	—	½	4	3	T	100
	2	75	15	T	5	—	—	—	—	—	—	—	—	T	5	T	T	100
	3	70	15	5	3	—	—	—	—	—	—	—	—	T	2	T	5	100
	4	40	43	5	2	—	—	—	—	—	—	—	—	T	5	T	T	100

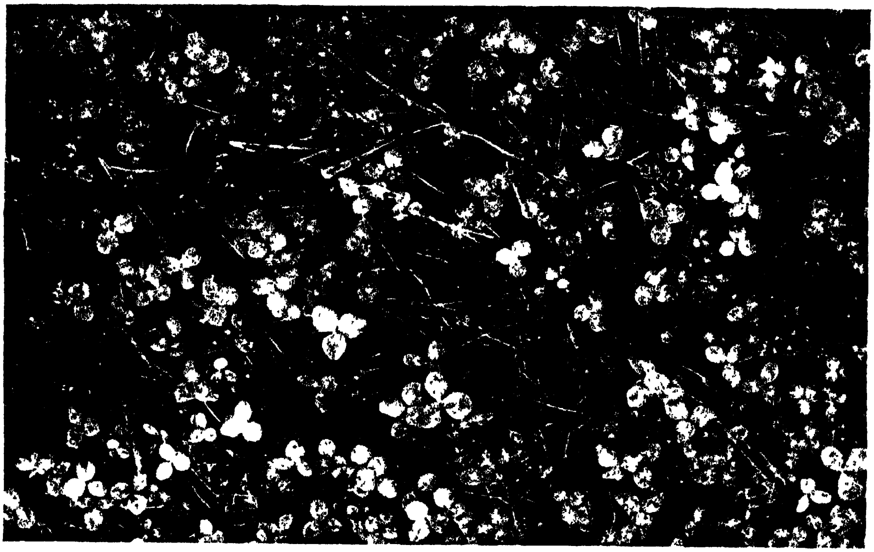
Other grasses = Perennial rye-grass, cocksfoot, timothy, crested dogstail and marsh foxtail.
Other herbs = Field woodrush, tormentil, heath bedstraw, heath rush, yarrow, buttercup, hawkbit, mouse-ear chickweed, dandelion, daisy and bird's foot trefoil.

Table 7. *The percentage contribution of (a) native grasses. (b) volunteer grasses. (c) wild white clover and (d) miscellaneous herbs to the aggregate season's yield for each plot*

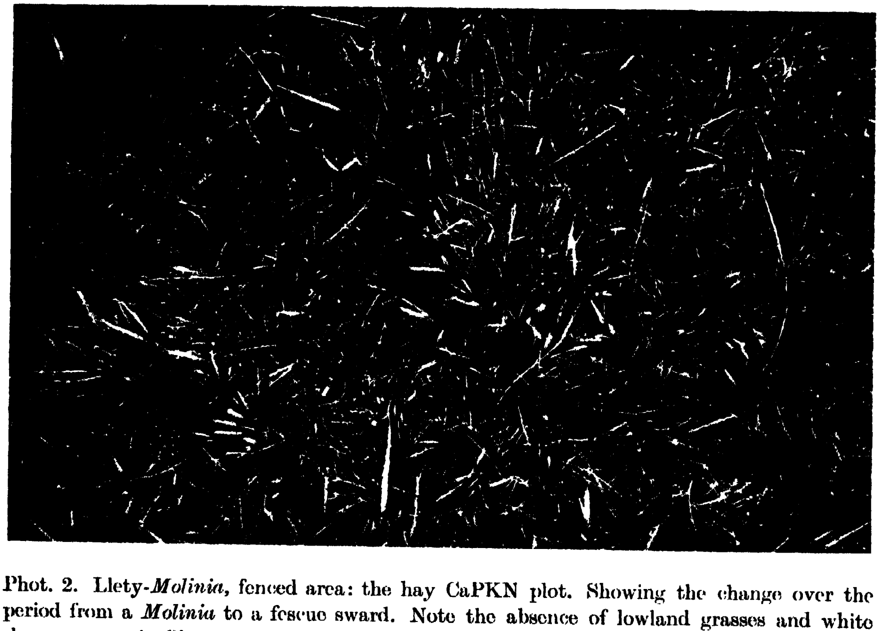
	Bwlchrosser					Llety-fescue					Llety-*Molinia*				
		Volunteer species					Volunteer species					Volunteer species			
Plot	Native grasses	Grasses	Wild white clover	Miscellaneous herbs	Total	Native grasses	Grasses	Wild white clover	Miscellaneous herbs	Total	Native grasses	Grasses	Wild white clover	Miscellaneous herbs	Total
CaPKN	49·8	36·0	14·2	T	100	32·5	40·1	27·4	T	100	2·9	57·1	40·0	T	100
PKN	57·8	42·2	T	T	100	95·4	4·6	—	T	100	58·3	41·7	—	—	100
Ca	30·7	52·5	14·6	2·2	100	58·3	15·1	19·3	7·3	100	14·1	39·2	45·5	1·2	100
P	60·4	17·1	21·5	1·0	100	80·8	9·4	4·4	5·4	100	86·7	13·2	—	0·1	100
Control	93·4	2·2	T	4·4	100	91·0	—	—	9·0	100	94·0	—	—	6·0	100
Hay CaPKN	—	—	—	—	100	87·8	7·1	—	5·1	100	100·0	T	—	T	100
Hay control	—	—	—	—	100	94·4	—	—	5·6	100	72·4	—	—	27·6	100
Cage	84·2	—	—	15·8	100	84·7	—	—	15·3	100	93·7	—	—	6·3	100

in dominance, with the result that this plot had the greatest percentage of native grasses of all the treatments in its aggregate yield. This P plot, however, had by far the greatest percentage of wild white clover in its herbage, although in actual yield this species was slightly below that of the clover in the CaPKN plot. The yield of the control plot was composed of approximately half fescue and half bent, but even in this unmanured plot rough-stalked meadow grass had gained a footing. The clover, however, did not rise above a trace in productivity. Heath grass persisted in this control plot, and the miscellaneous herb yields were greater than in the treated plots, with the exception of Ca. An examination of the open hill herbage as represented by the "cage" sample shows that there was a much higher percentage contribution of miscellaneous herbs and correspondingly a lower percentage of grass in the open hill compared with the fenced control plot, as seen in Table 7, while Table 4 shows that this grass contained more fescue and less bent than did the control herbage. These differences suggest that the herbage of the fenced Control plot had been decidedly influenced by the close and regular grazing of the treatment. With regard to the "other grasses" in the Bwlchrosser yields, the perennial rye-grass, cocksfoot and timothy composing this category had entered by 1939 to the extent of a trace of each.

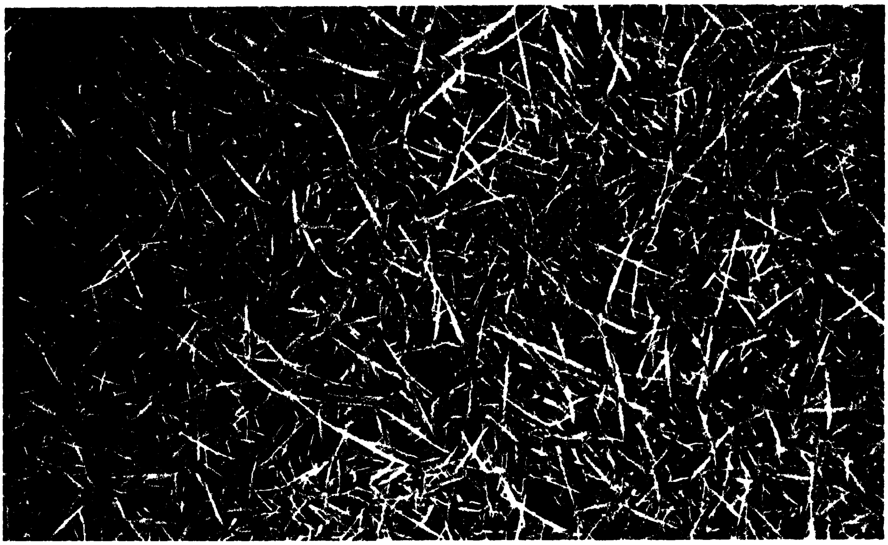
The yields of individual species at the Llety-fescue centre given in Table 5 show a very different botanical composition from those at Bwlchrosser for the majority of the plots, although the composition of the swards at the two centres in 1930 was of the same type. The aggregate season's yield of the pasture CaPKN plot at Llety-fescue was chiefly composed by 1939 of bent, rough-stalked meadow grass and wild white clover in very similar amounts. Fescue had diminished to little more than a trace, and there were scarcely any miscellaneous herbs. Smooth-stalked meadow grass contributed to the yield of volunteer species which together amounted to 67½% of the total yield from the plot. The PKN plot at this centre was unique in consisting almost entirely of bent, notwithstanding the fact that the herbage at the commencement of the trial contained more than three times as much fescue as bent. Only very small quantities of volunteer grasses appeared in this plot, and no clover. The Ca plot yielded a balanced herbage both in regard to the fescue-bent relationship and to a blend of volunteer species of which wild white clover was by far the heaviest yielding. The relatively high yield of yarrow is noticeable in this plot. Bracken was originally plentiful in this and the PKN plot, but the experimental treatment eliminated it after some years. The P plot was similar to the PKN in that bent was the dominant species in the herbage. There was over 9% of volunteer grasses, and over 4% of clover in the aggregate yield of this plot. Yarrow was again the chief contributor of the miscellaneous herbs. The herbage of the pasture control plot at this Llety-fescue centre resembled the control at Bwlchrosser in its aggregate yield, being chiefly composed of fescue and bent in approximately equal amounts. Heath grass and sweet vernal



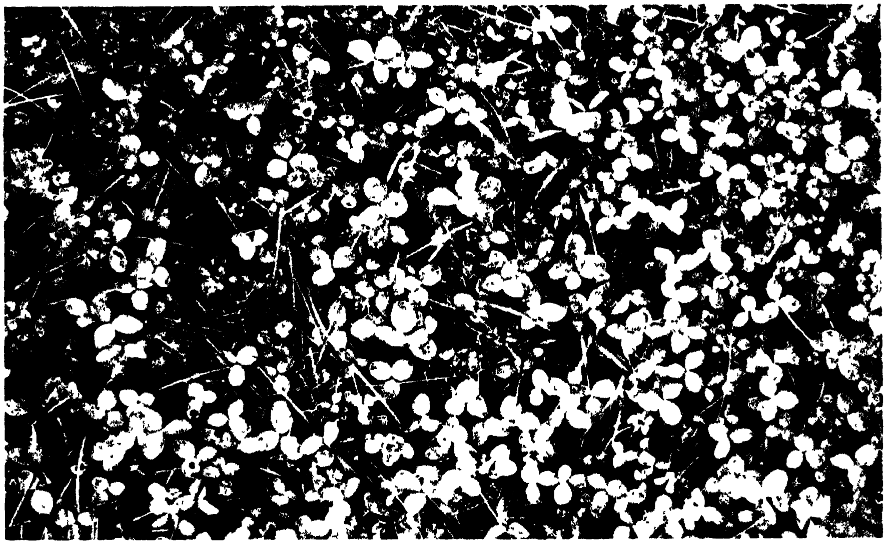
Phot. 1. Llety-*Molinia*, fenced area: the pasture CaPKN plot. Showing the improvement from a natural *Molinia* sward brought about by lime, artificial manures and controlled sheep grazing over a ten-year period—1930 to 1939.



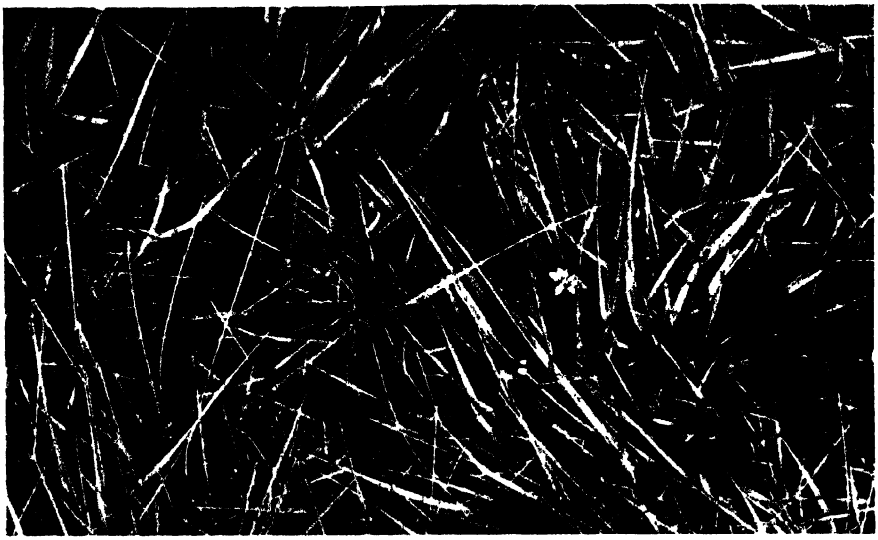
Phot. 2. Llety-*Molinia*, fenced area: the hay CaPKN plot. Showing the change over the period from a *Molinia* to a fescue sward. Note the absence of lowland grasses and white clover as seen in Phot. 1, although the manuring was similar for pasture and hay CaPKN plots from 1931 onwards.



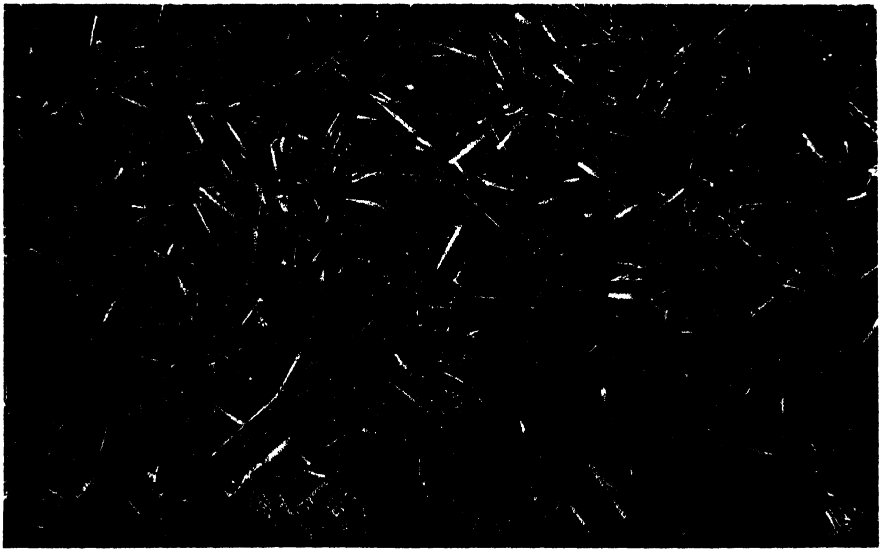
Phot. 3. Llety-*Molinia*, fenced area: the appearance of the PKN pasture plot by August 1939. Bent became dominant in the herbage, but certain lowland grasses gained an entry. Note the absence of wild white clover. The manures were superphosphate, kainit and sulphate of ammonia as for the CaPKN plot, but no lime.



Phot. 4. Llety-*Molinia*, fenced area: the Ca (lime) pasture plot by 1939. The herbage resembled the pasture CaPKN plot in its "lowland" character, but the flora was far more mixed, both as regards grass and miscellaneous species. Calcium carbonate was applied at the rate of 2 tons per acre in 1930, and again in 1935.



Phot. 5. Llety-*Molinia*: a "close-up" of the natural *Molinia* sward adjacent to the plots and representing the herbage in 1930 prior to treatment. The leaves of *Nardus stricta* and the flowers of heather can be seen among the leaves of the *Molinia caerulea*.



Phot. 6. Llety-*Molinia*, fenced area: the pasture control plot by 1939. This plot was grazed, but no artificial manures were given. *Molinia* still contributed one-quarter of the yield in 1939, whereas this species had disappeared within two to three years under complete manuring. Contrast with Phot. 5 shows that controlled grazing had improved the herbage.

contributed in appreciable quantities, and there was 9% of miscellaneous herbs. There were no volunteer grasses or clover present. The composition of the season's yield of the CaPKN hay plot at this centre differed very widely from the corresponding pasture plot in having fescue as the chief species, and only 7% of volunteer grasses as compared with 40% in the pasture plot; also in possessing no clover. The manuring was the same in both instances, except that the hay plots were commenced a year later than the pasture plots; the absence of the grazing animal in the hay-aftermath plots has therefore been the crucial differentiating factor. The yield of the hay control plot was composed entirely of native species. Fescue was the greatest contributor, as in the manured hay plot.

The composition of the open hill, or "cage", sample was of fescue, bent and heath grass in somewhat similar relationships as in the hay control yield, but there was present a much higher proportion of miscellaneous herbs, as is indicated in Table 7. With regard to the entry of volunteer grasses into this centre subsequent to 1937, smooth-stalked meadow grass appeared in 1938, and traces of perennial rye-grass, crested dogstail, meadow foxtail and annual meadow grass in 1939.

Considering now the botanical composition of the 1939 season's yield at the Llety-*Molinia* centre given in Table 6, the details of the pasture CaPKN herbage are one of the most remarkable features of the trial. As previously mentioned, volunteer grasses and wild white clover had increased to such an extent by 1937 that they comprised 92% of the total tillers of the sward. The yield in 1939 was therefore composed almost entirely of volunteer species, and the fescue and bent together with the trace of miscellaneous herbs amounted to less than 3%. Rough-stalked meadow grass and white clover were the major contributors to the aggregate yield.

Photographs were taken of the herbage of certain plots in August 1939, and Phot. 1 illustrates this pasture CaPKN plot at the *Molinia* centre. It is difficult to realize that such an improvement from a natural *Molinia* sward could be brought about simply by manuring and controlling and intensifying the grazing, and without having recourse to cultivating and the sowing of seeds. The contrast is readily seen in Phot. 5, which is a "close-up" of the adjacent *Molinia* sward. The flower heads seen in Phot. 5 are those of heather.

The yield of the PKN enclosed plot at this centre resembled this treatment at the other centres, in that bent was the dominant species. This plot had become almost pure bent under the treatment, but Yorkshire fog gained an entry and spread rapidly in one part of the plot. This was followed by rough-stalked meadow grass and annual meadow grass, with the result that these three volunteer grasses contributed over 40% of the yield in 1939. It is noteworthy that in contrast to the CaPKN plot there was absolutely no clover in the PKN herbage. The appearance of the sward is shown in Phot. 3. The herbage of the Ca plot at this *Molinia* centre had become almost as "lowland" in character as that of the CaPKN plot, Yorkshire fog, the three meadow grasses and white clover contributing 86% of the aggregate yield. Of this quantity 45% was composed of white clover. This was the highest percentage contribution of clover of any plot in the trial, but in actual yield the amount of clover was lower than that in the CaPKN plot of this centre. A very mixed flora of native species, volunteer grasses and clover, and volunteer miscellaneous herbs composed the yield of this plot, but in the summer of 1939 the clover dominated the appearance of the herbage, as is seen in Phot. 4. The majority of the lowland miscellaneous herbs given at the foot of Table 6 were present in this Ca plot. The yield of the P plot consisted mainly of bent and fescue. Yorkshire fog, rough-stalked meadow grass and annual meadow grass together contributed 13% of the yield, however, but wild white clover had not gained an entry. Sweet vernal contributed appreciably to the yield of this plot. Of the grasses which gained an entry into these manured plots during the recent years of the trial, perennial rye-grass appeared in 1938, and timothy, cocksfoot and slender foxtail in 1939. The herbage of the pasture control plot is notable in that *Molinia* still contributed approximately 25% to the yield, even by 1939. Ten years of controlled and hard grazing without the addition of manures had not enabled the fescue and bent entirely to replace the *Molinia*, but with complete fertilization this had taken place within two or three years. The amount of *Nardus*, heath-grass, *Carex* species and heather was appreciable in the yield of this control plot, and the same remarks apply to these species as to the presence of the *Molinia*. The herbage had decidedly improved from its original composition, however, as can be seen by reference to Table 1. The mingling of the *Molinia* leaves with the other species can be clearly observed in Phot. 6, which illustrates this sward.

The composition of the yield of the hay CaPKN plot consisted almost entirely of sheep's fescue with small quantities of *Molinia* and bent. Native species, with the exception of a trace of Yorkshire fog, therefore, comprised the entire herbage. This fact compared with the herbage of the pasture CaPKN plot, where the manuring had been identical, save that it had commenced one year earlier on the pasture, constitutes a most striking contrast. The change from a *Molinia* sward to one of fescue and bent took place in both these CaPKN plots, but whereas under hay with aftermath conditions the change up to the present time has not proceeded further, the effect under grazing conditions has resulted in a second change, for now (after ten years) what is tantamount to a lowland sward has developed. A study of Phot. 2, which is of the hay CaPKN plot and of Phot. 6, the pasture plot, illustrates the contrast. The yield of the hay control plot was composed of *Molinia* and sheep's fescue in approximately equal amounts. Here there was a higher percentage of *Molinia* than in the pasture control plot, and there was only a trace of bent. The amount of bilberry and heather had actually increased under this system of cutting for hay and aftermath. This plot gave the smallest yield and the poorest botanical composition of all plots at the three centres. A comparison of the percentage contribution of the miscellaneous herb group to the yield of this hay control plot, and that of the open hill, or "cage" sample, as seen in Table 7, shows that the percentage for the latter was less than one-quarter of the control figure. This was caused by the spread of the bilberry and heather in the hay plot as mentioned above.

(*d*) *Seasonal yields.* The final columns of Tables 4 6 show the total yields at each cut, which constitute the seasonal yield from the plots. The data for Bwlchrosser given in Table 4 show that the CaPKN plot had by far the most even distribution of yield over the four cuts, namely, 22 May, 14 July, 5 September and 30 October. This was chiefly due to the even yield of the fescue in the herbage of this plot. The PKN plot gave a large yield in July for its second cut, mainly owing to bent and rough-stalked meadow grass, but its yields in May and October were low in comparison. In the case of the Ca plot, fescue and the smooth- and rough-stalked meadow grasses were mainly responsible for this plot giving a good yield at the last cut, but the much lower yield of wild white clover at this late period influenced the yield of this plot, and also of the P plot. The yields of this latter plot were fairly well distributed. The control yield was the most unevenly distributed of the plots at this centre. Owing to the behaviour of fescue and bent the yield was five times as large for the second cut in July as for that in May, and its October cut was higher than the cut on 5 September, and slightly higher than that in July.

The seasonal yield data for the Llety-fescue plots given in Table 5 show that the yield of the CaPKN pasture plot for the second cut was very much greater than for the other cuts. The bent and smooth-stalked meadow grass in the herbage both gave their greatest yield at this date, but the yield of rough-stalked meadow grass was exceeded by the first cut, and that of the clover was only slightly in excess of the yield for the third cut taken in September. The seasonal distribution of the PKN yield was poor as both the first and the fourth cuts were small in comparison with the two mid-season cuts. This was caused by the optimum yields of the chief component in its herbage, bent, occurring in July and early September. The Ca and P plots gave better distributions of their yields, and the end-season yield of the Ca plot was the largest of all at this centre. The pasture and hay control plots gave good seasonal distributions, except for the comparatively small yield of the pasture plot in May, due to the low productivity of all its component species. The CaPKN hay plot gave the best distribution of yield of all the manured plots at this centre, for there was regularity on each side of its peak period in July.

The seasonal yield data for the Llety-*Molinia* centre given in Table 6 shows that the CaPKN pasture plot gave the greatest proportion of its total yield at the two mid-season cuts. There was a sharp drop in productivity of the volunteer lowland grasses, and white clover from 5 September to 30 October cut. The distribution of the PKN yield was still more unbalanced in that it gave the major part of its season's yield in July, the chief species in the herbage producing their optimum growth at that time. The Ca plot of this centre gave the best distribution of yield over the four cuts of the season, and, as in the case of the Ca plot at the Llety-fescue centre, it gave the largest yield of all the plots on 30 October. The yield for the first cut of the P plot was very small in comparison with the remaining cuts. The bent of which it was mainly composed did not yield well until the second cut, which was taken in July. The pasture control plot at the *Molinia* centre gave its largest yield at 30 October cut, when it was more than double the yield at any of the preceding cuts. All the species in its herbage contributed to this fact. The distribution of the yields of the CaPKN and control hay plots were both characterized by having much larger yields for the second and fourth cuts than for the remainder. The data show that the majority of the species composing their herbage reacted in this manner.

The open or freely grazed plots

As previously mentioned, the manuring was carried out on the open hill at each centre, as well as in fenced plots, and botanical data together with palatability data have been recorded throughout the trial. These results up to and including the year 1937 have been summarized from earlier reports, and given in a preceding portion of this paper. The recent data, extending over the period 1937 to 1939, are given in Tables 8-10. The data for 1937 have been extracted from the latest report (4) for the purpose of convenient comparison.

The particulars for Bwlchrosser given in Table 8 show that there was a great increase of wild white clover from 1937 to 1939 in the open CaPKN, Ca and P plots. The clover increased very slowly in the P plot up to 1937, but its increase during the next two years was so rapid that its percentage number of tillers exceeded the tillers of the clover in the CaPKN plot. White clover had not increased at all under PKN treatment, there being no more present in the herbage after ten seasons of manuring than in the control, or unmanured, hill sward. These plots at Bwlchrosser remained fescue-bent in their composition with regard to their dominant grass species, but smooth-stalked meadow grass gradually contributed appreciably to the herbage of the treated plots, especially to the Ca plot, by 1939. Yorkshire fog was also encouraged by the lime treatment, but its proportions decreased as the meadow grass and clover increased. A very noticeable factor in the composition of this Ca plot was the large proportion of miscellaneous herbs in its herbage. *Carex*, yarrow and pearlwort were the chief contributors, the leaves of *Carex* being particularly noticeable at some little distance. The unmanured portion of the sward, adjacent to the manured plots and considered as a control, contained large proportions of sheep's fescue, heath-grass, tormentil and other herbs.

These open plots at Bwlchrosser have been among the most interesting of the trial in that marked differential grazing occurred among them at an early

Table 8. *The composition of the open plots at Bulchrosser for the years* 1937–9, *based on a percentage tiller estimation*

Plot	Year	Fine-leaved fescue	Bent (*Agrostis* spp.)	Heath grass	Sweet vernal	York-shire fog	Smooth-stalked meadow grass	Rough-stalked meadow grass	Annual meadow grass	Wild white clover	Bird's foot trefoil	Field wood-rush	Tor-mentil	*Carex* spp.	Yarrow	Other herbs	No. of tillers per 6 × 6 in.
CaPKN	1937	47	23½	T	½	1	7½	—	—	19	—	T	T	T	T	1½	402
	1938	43	37½	—	T	T	2½	1½	½	15	—	T	T	T	T	T	420
	1939	37½	20	—	T	T	5	2	½	35	T	T	T	T	T	T	380
PKN	1937	45	49	½	T	T	2½	—	—	1	—	1	½	T	—	½	427
	1938	51½	45½	T	½	T	½	—	—	T	—	1½	½	T	—	T	450
	1939	40½	55	T	T	T	3	—	—	T	—	½	1	T	T	T	410
Ca	1937	36½	13½	1	2½	4½	5	2	½	8	½	1	2	7½	1	14½	401
	1938	37½	27	½	½	2½	8½	T	½	6½	1	1½	T	3	4	7	430
	1939	16	25	T	½	1½	15	T	½	18	½	T	T	10	8	5	395
P	1937	11½	58½	T	T	T	½	T	T	19½	3	½	½	½	—	5½	478
	1938	37	40½	½	T	T	½	T	—	18	½	T	T	½	½	2	465
	1939	18½	34	T	½	T	1½	T	—	42½	½	T	T	½	T	2	400
Control	1937	33½	44½	11½	2	—	—	—	—	½	1	T	3½	1	T	2½	393
	1938	69	21½	3½	½	—	T	—	—	T	½	½	2	1	T	1½	425
	1939	57	30	5	½	—	T	—	—	½	½	T	3	1	T	2½	430

Other herbs = heath bedstraw, mountain pansy, mouse-ear hawkweed, heather, bilberry, pignut, eye-bright, ribgrass, pearlwort, mouse-ear chickweed, buttercup and daisy.

Table 9. *The composition of the open plots at Llety-fescue for the years* 1937–9 *based on a percentage tiller estimation*

Plot	Year	Fine-leaved fescue	Bent (*Agrostis* spp.)	Heath grass	Sweet vernal	*Molinia caerulea*	Wild white clover	Field wood-rush	Tor-mentil	Heath bed-straw	*Carex* spp.	Bilberry	Heather	No. of tillers per 6 × 6 in.
CaPKN	1937	65½	32	T	—	—	—	2	½	—	T	—	—	468
	1938	59½	38	T	—	—	—	2½	T	—	T	—	—	460
	1939	50	45	T	—	—	—	5	T	—	T	—	—	470
PKN	1937	44	55½	T	T	—	—	½	T	T	—	—	—	271
	1938	54	45	T	1	—	—	T	T	T	—	—	—	290
	1939	35	65	T	T	—	—	T	T	T	—	—	—	280
Ca	1937	70½	23	T	—	T	T	1	3½	T	½	½	1	469
	1938	75	22	T	—	T	T	½	2	½	T	T	T	475
	1939	55	37½	T	T	T	½	T	5	2	T	T	T	450
P	1937	74	16½	T	—	3½	—	1	3	1	—	1	T	429
	1938	72½	19	T	—	1	—	T	3	1½	—	3	T	450
	1939	60	27½	T	—	1	—	T	5	2½	T	4	T	455
Control	1937	59	18½	2	T	3½	—	½	3½	4	T	1	8	395
	1938	60½	23	1½	T	1½	—	½	4	2	T	T	7	410
	1939	55	24½	2	T	1½	—	T	7	5	T	T	5	400

Table 10. *The composition of the open plots at Llety*-Molinia *for the years* 1937–9 *based on a percentage tiller estimation*

Plot	Year	*Molinia caerulea*	Fine-leaved fescue	Bent (*Agrostis* spp.)	*Nardus stricta*	York-shire fog	Wild white clover	*Carex* spp.	Bilberry	Heather	*Scirpus caespitosus*	*Juncus squarrosus*	Tor-mentil	Other herbs	No. of tillers per 6 × 6 in.
CaPKN	1937	21½	76	1	1½	—	—	—	—	—	—	—	—	T	403
	1938	20	72	4	4	—	—	—	—	—	—	—	T	—	385
	1939	25	66	5	4	—	T	—	—	—	—	T	T	—	390
PKN	1937	26½	38	24	10½	1	—	T	—	—	—	—	—	—	412
	1938	22	50½	16	9	T	—	T	—	—	2½	—	—	—	450
	1939	20	60	15	5	—	—	—	—	T	T	T	T	—	450
Ca	1937	28½	67½	2	1½	—	—	T	T	—	—	—	½	—	435
	1938	35	61	2	2	T	—	T	—	—	—	—	T	T	420
	1939	50	42	1	2	5	T	T	—	—	—	T	T	T	380
P	1937	31½	63½	4½	—	—	—	T	½	—	—	—	T	T	425
	1938	36	59½	2	2	—	—	T	T	—	—	½	T	—	410
	1939	50	38	2	5	T	—	T	T	T	T	5	T	—	375
Control	1937	60½	21½	1	½	—	—	T	7½	1½	3½	4	—	T	320
	1938	64	26½	2	3	—	—	T	½	T	1	3	T	T	345
	1939	64	10	1	10	—	—	T	5	4	1	5	T	T	325

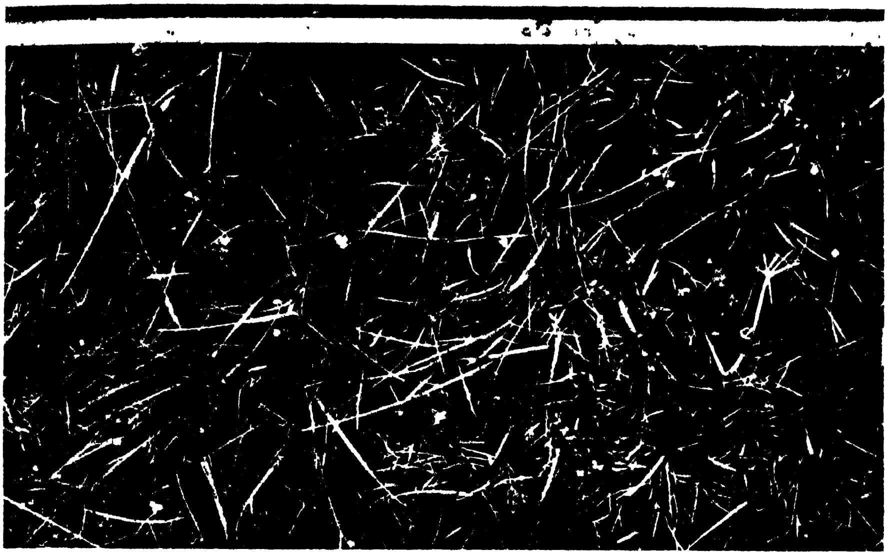
Other herbs = heath bedstraw, field woodrush, mouse-ear chickweed, sheep's sorrel and pearlwort.

date, and it has continued so throughout the ten-year period. This has resulted in clear-cut changes in the botanical composition and appearance of the individual plots. A photograph was taken of their swards in August 1939 in order to illustrate the difference among the treatments. Sheep and cattle graze this hill sward over the entire year, and they discovered the effect of the manures and the lime on the open plots within a year of the initial application in 1930, although each plot was only 1/100 acre in size. The animals always kept the open CaPKN plot at Bwlchrosser absolutely closely grazed. The appearance of its herbage is illustrated in Phot. 9, in which the large amount of wild white clover and the general fineness of the leafage can be clearly seen. The PKN plot, on the other hand, was the poorest grazed of the manured open plots during the recent years of the trial, and bracken infested the sward. This bracken was a continuation of a large bracken-infested area which extended into the adjoining Ca and CaPKN plots. On these latter plots, however, the bracken almost disappeared under the effect of the close grazing, and response to fertilizers and/or lime. This PKN plot is illustrated by Phot. 10. The view is along the diagonal of the plot and the plot-area is indicated by means of an outstretched cane. The interesting fact is that a sharp line of demarcation is seen on the right-hand side of the photograph between the bracken-infested PKN plot and the hard-grazed Ca plot. This view, incidentally, shows the type of country in which this investigation was undertaken.

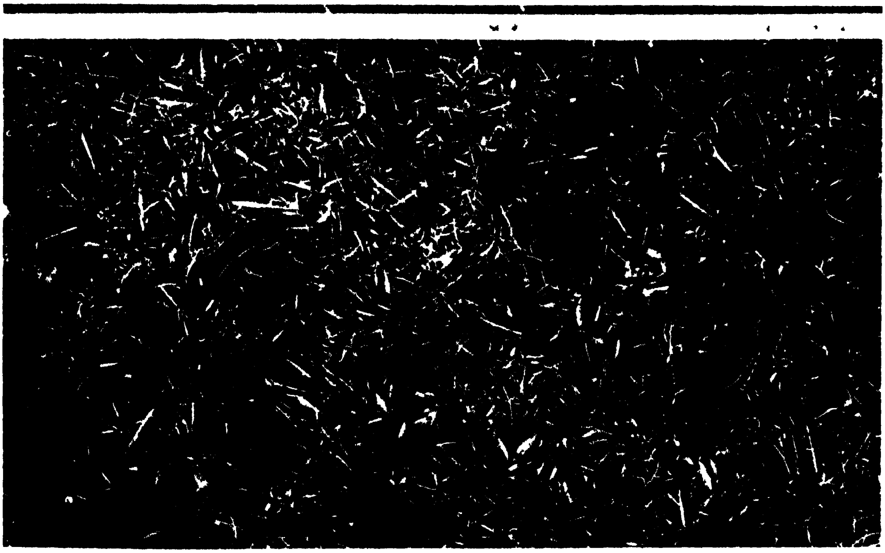
The Ca plot came next in order of palatability to the CaPKN plot, and its sward is illustrated in Phot. 8. The mixed nature of the herbage is discernible and the wild white clover is in evidence. As already stated, the grazing of the P plot was poor in the early years of the trial, but when the clover in its herbage increased, the grazing became very much harder. This P sward was a mass of white clover by 1939. The close grazing to which the palatable plots were subjected led to extremely small leaves in the wild white clover. The leaves of the grasses were also very fine, although these are not as easily distinguishable as the clovers in the photographs. The sward of the natural open hill, or control plot is seen in Phot. 7, and several species of its composition, as given in Table 8, can be distinguished, notably the heath-grass, which stands out against the darker fescue and bent, and also the tormentil. This control plot has always been grazed less than any of the treated plots, and in order to show the relationship of the degree of grazing between unmanuring and the application of manures and lime the statement hereunder is repeated from a previous report (4). The data consist of relative marks on a scale of 0–10 given for grazing in 1937, compared with those given in 1933.

Bwlchrosser

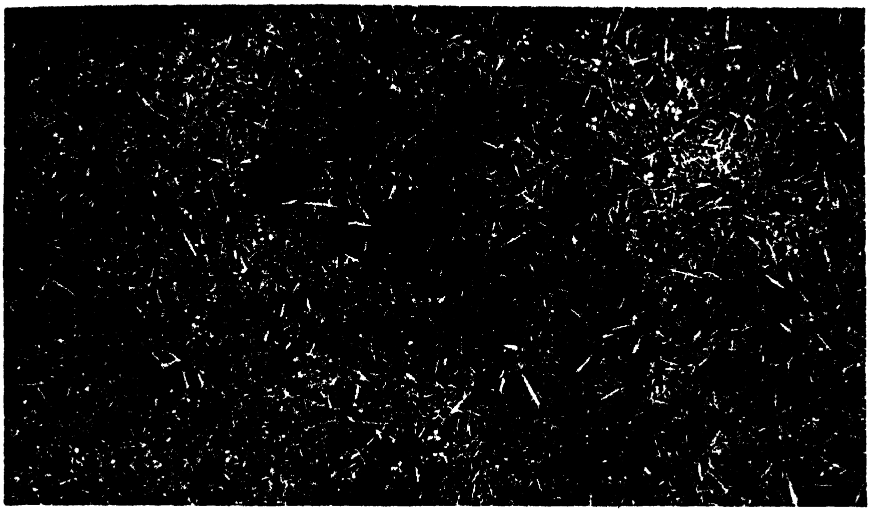
Open plots	1933	1937
CaPKN	10·0	10·0
PKN	7·9	5·0
Ca	8·9	9·0
P	5·7	8·5
Control	2·7	2·5



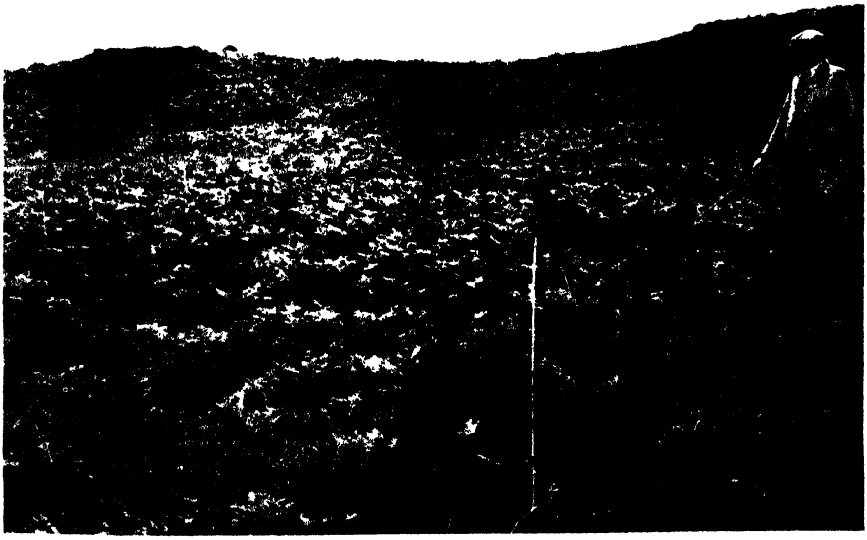
Phot. 7. Bwlchrosser, open area: the open hill or control plot. The herbage is composed of native grasses and miscellaneous herbs—fescue, heath-grass and tormentil being particularly in evidence. The degree of grazing has always been less than on the manured plots.



Phot. 8. Bwlchrosser, open area: the Ca (lime) plot by 1939. This open plot had the same two applications of calcium carbonate as had the fenced Ca plots. At this centre it was the next sought after to the CaPKN plot. Note the mixed flora of clover, grass and herbs.



Phot. 9. Bwlchrosser, open area: the CaPKN plot by August 1939. Sheep and cattle had access to these open plots since their commencement in 1930. This CaPKN plot was always kept in a hard grazed condition. Wild white clover spread rapidly, and the close grazing led to very small leaves, both in the clover and the grasses.



Phot. 10. Bwlchrosser, open area: the PKN plot by 1939. Of late years the poorest grazed of the open plots and now bracken-infested. The plot-area is indicated by the outstretched cane. Note the contrast with the hard grazed Ca (lime) plot on the right-hand side.

It will be seen that the control, or unmanured, sward was grazed to only half the extent of even the relatively unpalatable PKN in 1937. The data also show the decreasing relative palatability of the PKN plot compared with the Ca and P plots as these latter became more densely covered with clover during the intervening years, and consequently became more on a level with the CaPKN plot. The differential grazing data on these plots up to 1939 merely indicated the still closer degree of uniformity between the CaPKN, Ca and P plots.

The data for the open plots at the Llety-fescue centre are given in Table 9. The smaller number of species present in the herbage of these higher and more exposed plots, compared with Bwlchrosser, is noticeable. These plots at Llety have retained their original fescue-bent composition and the dominance of the former species with the exception of the marked increase of bent in the PKN plot by 1939. There have been botanical alterations in the manured plots, however, as can be seen by the smaller proportion of heath-grass and of some of the miscellaneous herbs, compared with the control plot, or unmanured sward, and also the appearance of a trace of wild white clover in the Ca plot. More particularly the effect has shown itself in the differential grazing among the plots. At this centre the CaPKN has been the hardest grazed plot and the PKN came next in order. The Ca plot was grazed to a lesser extent than the PKN plot, and was followed by the P plot. All the treated plots were decidedly more palatable than the control herbage, and the palatability of the Ca and P plots increased during the later years of the trial. The difference in the order of proportional grazing at this centre, compared with Bwlchrosser, has been apparently caused by the wild white clover factor, only a trace of this species occurring in the open plots at Llety.

The composition of the open plots at the Llety-*Molinia* centre are given in Table 10. There has occurred a marked change in the botanical composition of the CaPKN and PKN plots compared with the control. The proportion of *Molinia* in these two plots has decreased to approximately one-third, and there has been a corresponding increase of fescue. There was also a marked increase of bent in the PKN plot, compared with the other treatments. Yorkshire fog and wild white clover appeared voluntarily in certain of the treated plots, but the latter species only occurred as a trace in the CaPKN and Ca plots by 1939.

It will be noted that all the fertilized plots had lower proportions of miscellaneous herbs in their composition compared with the unmanured herbage. At this centre the order of preferential grazing was the same as at the Llety-fescue centre, namely, the CaPKN and PKN plots were the hardest grazed, and to a much more intense degree than the Ca and P plots, and of these the Ca was harder grazed than the P. In recent years the Ca and P plots have been grazed less heavily than formerly, and this fact would account for some increase of *Molinia* in their herbage from 1937 to 1939 as seen in Table 10.

DISCUSSION AND SUMMARY OF THE YIELD AND BOTANICAL SECTION

One of the most interesting features of the experiment has been the yield data obtained in 1939. These data are the outcome of ten seasons of manuring, representing in the aggregate very heavy dressings, and it is perhaps not surprising therefore that the results have been very considerable.

The details of these yields have shown that superphosphate alone gave nearly three times the pasture yield of the unmanured plot at each centre, yet this treatment provided the lowest yield of all the treatments. At the opposite extreme, complete manuring including lime exceeded the unmanured by nearly five times at Bwlchrosser, by four at Llety-fescue and by nearly six and a half times at the Llety-*Molinia* centre. It is interesting that the order of increasing yield was the same at each centre, namely, P, Ca, PKN and CaPKN. The fact that the yields from the lime and completely manured plots at the *Molinia* centre were far greater relative to the unmanured pasture plot than were the corresponding plots at the other centres is in agreement with other current work on *Molinia* and fescue soils at Llety (6). These results indicate that inherently more fertile conditions prevailed in the *Molinia* area, and this was especially marked when limestone had been included in the manurial dressing. Comparison between the enclosed plots of the several centres is complicated by the occurrence of volunteer species, and clear-cut contrasts in yield between manured and unmanured natural herbage can only be made in a few instances at this date. Also if the early period of yield recording, 1930 to 1933, is considered from this standpoint, the position is still complicated, for during that period the *Molinia*, which comprised the bulk of the original herbage at that centre, was being rapidly killed out by the periodical hard grazing. Colonization by the sheep's fescue and bent was taking place at the same time, but this shift in botanical composition did not fully set off the decrease in *Molinia* during the early period of change. Consequently, as previously explained, the actual yields of the treated plots at the *Molinia* centre were lower than at the fescue-bent centres, but the relative yields of the treated plots compared with the *Molinia* pasture control were considerably higher which shows that the manures and lime had their greatest effect on the *Molinia* soil.

The entry of volunteer grasses and wild white clover into certain plots and the very striking effect they have had upon yield and composition of the herbage is from one aspect perhaps the most significant result of the experiment. At the time when any particular lowland species was first noted, only a trace was discernible, but under the influence of the artificial manures and lime, when supported by intensive sheep grazing, they quickly spread by their creeping growth habit and formed large colonies. As has been mentioned in an earlier report (4) there were several means by which the seeds of these grasses and white clover could gain an entry into these hill plots. Seeds could have been dropped from the clothing and boots of the workers, from bags used for herbage samples and from the wool and possibly the droppings of the sheep. Certain of these lowland grasses have become established in the hay plots, from which sheep have been excluded. This shows that the former means of contamination have been responsible in this case. That the carriage of these seeds has been constantly active is proved by the almost yearly appearance of fresh species at every centre. No seeds of these volunteer species were present in the soils of these hill areas at the commencement of the trial, for it is known from an investigation into the buried viable seeds of these areas (7) that only the seeds of the native species were present in the soils. The data from the two Llety centres clearly show that the generous application of lime was the principal factor in promoting the establishment and subsequent growth of these lowland species, and that the addition of superphosphate, kainit and sulphate of ammonia ensured their maximum yield. The absence of lime in the otherwise completely manured plots has prevented colonization by wild white clover, and also the volunteer grasses have not been encouraged to the same extent. Data from the experiment at Llety previously referred to (6) have afforded evidence of the beneficial effect of lime on lowland species on these soils, particularly as to the voluntary appearance of wild white clover. the additional presence of basic slag resulted in greater success in this respect. Also Thomas (8) mentions the impossibility of successfully establishing seedlings from introduced seed on the Cahn Hill lands without the addition of phosphates and lime. With regard to the clover in the present experiment, it is reasonable to suppose that volunteer entry of the seeds of this species was general throughout the plots. Its failure to appear in the herbage of the enclosed PKN and control plots at each centre, and in that of the P plot at the *Molinia* centre can therefore be attributed to the direct effect of the manures, the grazing and the soil. This view is supported by the position in regard to clover at the Bwlchrosser centre. It will be remembered that a trace of this species was originally present, and therefore the volunteer factor was only of minor importance. Yet, throughout the whole period of the experiment, the clover remained but a trace under PKN and unmanured conditions, and the same was the case in the adjacent open plots although it flourished in all plots of the remaining treatments at this centre. The herbage of the P plot at the *Molinia* centre (at Llety) has remained strongly native in character, both in regard to fescue and bent, and in relative productivity. This has apparently precluded any entry of clover. Certain species of lowland grasses, on the other hand, have been able to become established and to increase under P and PKN manuring.

The species composing the majority of the herbage in the various cuts taken in 1939 were responsible for the seasonal distribution of the yield of any particular plot. The most outstanding instance has been that bent, which formed one of the chief species in many plots, usually gave its greatest yields at the two mid-season cuts. The effect of this is particularly noticeable in the

PKN treatment. The influence of the volunteer grasses in this respect has been to increase the yields at the first cut taken on 22 May, and in some instances to keep up the yields in the last cut taken on 30 October. The wild white clover has behaved in a similar manner to the bent in giving its greatest yields in July and early September. Among the individual treatments the lime plots have given some of the heaviest end-season yields. Lime by itself has produced the most varied flora of all the treatments, a fact which has been largely responsible for the good seasonal spread-over in the yield of plots so treated. The plots having large amounts of native species in their herbage, namely, the pasture controls and the manured and unmanured hay plots, have given distributions of yield very different from those of the manured pasture plots which contained large quantities of volunteer species. These native herbages have usually given their heaviest yields in July and in October.

The yields of the hay with aftermath plots at the Llety centres compared with the yields of the pasture plots have formed a great contrast. As has been previously stated, the four cuts made in 1939 were taken on hay and pasture plots alike. The presence of lowland species in the pasture CaPKN plots caused the wide differences in yield and composition, compared with the CaPKN hay plots, especially at the *Molinia* centre where the pasture plot gave almost six times the yield of the hay plot. At the fescue centre the pasture plot yielded slightly less than double the hay yield. The differences in yield between the pasture and hay unmanured plots which were all composed entirely of native species shows, however, that the larger yields have been obtained from grazing. This has been particularly so at the *Molinia* centre, for not only has the grass portion of the cut herbage been inferior to the pasture both in yield of individual species, and in the absence of certain species, but there has been a marked increase of heather and bilberry in the cut plot. This increase of heather where sheep have been excluded is in agreement with the investigation on the influence of sheep on hill grazings reported upon by Fenton (**9**). The actual yield of *Molinia* in the hay unmanured plot of the present experiment was slightly less than the yield of this species in the pasture plot, but the percentage contribution to the total yield was greater in the hay herbage. The *Molinia* in the hay-manured plot had decreased to a very small quantity, but in the correspondingly manured pasture plot it had long since disappeared altogether. The investigations of Jones on lowland swards provide interesting comparisons on this question of yield in regard to grazing *versus* cutting. Data from an unmanured bent sward (**10**) showed the superiority in yield of the grazed plots, and in a similar experiment on a marsh (**11**), *Molinia* gave heavier yields under cutting conditions than under grazing. That the pasture conditions have resulted in the largest yields under manuring on the hill swards investigated in the present trial is of great practical significance, for improved herbage under these hill conditions will be far more frequently used directly in the form of grazing than preserved as fodder in the form of hay.

The decrease of *Molinia* under both systems of management is an important factor, for the fescue and bent which take its place provide herbage of more economic value both as regards productivity and from the standpoint of palatability (**12**). The most rapid change from *Molinia* to fescue-bent took place in the completely manured pasture plots, and secondly in the manured hay plot. The change was less rapid in the Ca and P plots, and, as the 1939 data show, the pasture and hay unmanured plots were still composed of approximately one-quarter to one-third of this species. Even these amounts, however, are considerably less than the 71 % of *Molinia* in the herbage in 1930. Previous and current work at Llety on a *Molinia* sward involving periodical cutting (**5**, **6**) have brought about this botanical change, and it has been greatly accelerated by manuring. Detailed descriptions of *Molinia* and fescue-bent swards with their positions in the ecology of hill land have been given by Stapledon (**13**), in which publication also are given the percentage of rough and hill grazings for certain counties in Great Britain, of which the type of swards here under discussion form a considerable portion.

Changes in botanical composition took place in the manured plots of the open hill at each centre. The most marked of these were the great increases of wild white clover in the CaPKN, Ca and P plots at Bwlchrosser, and the decrease of *Molinia* in the CaPKN and PKN plots at the Llety-*Molinia* centre. With regard to bent, it is interesting to note that there were far greater proportions of this species in the open PKN plots at each centre than in the open CaPKN plots. A comparison with the herbage of the enclosed plots, however, shows that larger amounts of bent developed than of fescue as improvement took place. In this connexion it is of interest to note that Jenkin (**14**) found that an improvement in hill herbage was accompanied by an increase of bent. There was also in the open manured plots of the present experiment considerably more *Molinia* than in the enclosed plots. The reason for these differences in composition derived from free as opposed to controlled grazing is to be found in the fact that the latter plots were subjected to absolutely close and heavy grazing at regular intervals. The concentration of the sheep droppings and urine was undoubtedly an influence of the first importance.

The palatability of these open plots has, of course, been intimately connected with their changing botanical composition, and both factors are the outcome of the action from the fertilizers and/or lime. The most striking result was at Bwlchrosser. That the superphosphate plot which was of low relative palatability in the early years of the trial should in time become equal in this respect to the complete manure including lime plot and to the lime-alone plot conclusively shows the influence of wild white clover on palatability under these conditions. Also, the PKN plot at Bwlchrosser was equal to the lime plot in palatability during the first years of the trial, but it gradually became the least sought after; this was the case when clover developed in great quantity in the other treated plots, but remained merely a trace in this (the PKN) plot. At the Llety centres this influence was absent, owing to the non-leguminous herbage of the open plots. At these centres, therefore, the direct effect of the fertilizers and lime on palatability by reason of increased nutritive properties of the herbage can be seen. This is especially so at the fescue centre, for here there was the least botanical change among the open plots, but differential grazing was none the less definite and persistently uniform. The work of Beaumont on a permanent pasture (**15**) is in agreement with this finding; when interpreting the results of a palatability experiment with manures he considered that the higher content of nutrients in the vegetation of the limed and fertilized plots accounted for their greater palatability.

In conclusion, the main facts emerging from the foregoing data of this section are that improvements can be effected on fescue-bent and *Molinia* hill swards in terms of yield and botanical composition if the areas are fenced, manured and limed, and heavily grazed under a controlled system. Improvement in a lesser degree can be effected if such treated herbage is cut for hay and aftermath, instead of being grazed. In the majority of the fenced and closely grazed pasture plots improvement has been greatly enhanced by the unexpected appearance of lowland grasses and wild white clover. Even without fencing, however, considerable changes towards a better herbage can be brought about by manuring and liming the open hill swards. Yields have not been obtained under this open system, but the botanical results and the differential grazing following this treatment have clearly shown that improvement has taken place. It has taken several years from the volunteer entry of such plants as rough-stalked meadow grass and wild white clover to increase and dominate the herbage of some plots as they, and certain other cultivated species, have done by 1939. The rate of improvement in this instance has, therefore, been slow compared with cultivating the soil, and the sowing of seeds and manures, described by Griffith in a report of the Cahn Hill Improvement Scheme (**16**). The fact, however, that the same results in respect of the establishment and vigorous growth of cultivated species have occurred in certain heavily manured pasture plots in the present experiment where no soil cultivation or seed sowing has taken place is full of significance. It is extremely probable that had the unlooked for appearance of these species been forestalled by the deliberate sowing of their seeds in the early years of the trial, the economic results would have been greater by reason of a quicker rate of improvement in this direction. Moreover, the data have shown that even when no artificial fertilizers have been applied, the addition of lime to the soil in generous amount can effect the establishment and successful growth of these lowland grasses and wild white clover.

From the strictly ecological and scientific point of view the most significant results are firstly, that increased yield of mixed herbage resulting from any beneficial treatment whatsoever is a function of two factors: of the enhanced yield of each contributing species *per se*, and of a shift in the botanical composition towards species with higher inherent yielding abilities. Moreover, any treatment to which a mixed herbage is subjected, whether such treatment be manurial or *via* altered management of the grazing animal, will necessarily occasion an alteration both quantitative and qualitative in the botanical composition of the herbage. Starting on native hill vegetation the general tendency of beneficial treatment is to increase the proportion of bent at the expense of other species, and then, if the treatments are generous, drastic and long continued, for volunteer species to gain entry and gradually to take a dominant place in the vegetation. Of both practical and scientific significance is the fact that without fail the most striking advances in yield, and the most striking, as well as the most beneficial, changes in botanical composition have taken place where abundant droppings of the sheep and abundant urination (i.e. on the enclosed and heavily grazed plots) have supported the generous application of lime and artificial manures. Under these conditions the changes brought about in a period of ten years have been remarkable. Their very magnitude shows that soils inherently low in available lime, phosphates and nitrogen, and a natural vegetation incapable of sustaining a large head of sheep, and therefore rendering impossible the heavy spread of urine and droppings, are factors greater than climate in determining the natural vegetation of our hill grazings. In short it is true to say that the vegetation of our open hills is what it is because for one very important reason it is incapable of sustaining (in its present floristic make-up) a larger head of stock than it does in fact sustain.

ACKNOWLEDGEMENTS

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APPENDIX

The scientific and common names of the species mentioned in this paper

Anthoxanthum odoratum L.	Sweet vernal
Alopecurus pratensis L.	Meadow foxtail
A. geniculatus L.	Marsh foxtail
Phleum pratense L.	Timothy grass
Agrostis sp.	Bent grasses
Aira flexuosa L.	Wavy hairgrass
Holcus lanatus L.	Yorkshire fog
Triodia decumbens Beauv.	Heath-grass
Cynosurus cristatus L.	Crested dogstail
Molinia caerulea Moench.	Flying bent
Dactylis glomerata L.	Cocksfoot
Poa pratensis L.	Smooth-stalked meadow grass

Poa trivialis L.	Rough-stalked meadow grass
P. annua L.	Annual meadow grass
Festuca ovina L.	Sheep's fescue
F. rubra L.	Red fescue
Lolium perenne L.	Perennial rye-grass
Nardus stricta L.	Matgrass
Trifolium repens L.	White clover
T. pratense L.	Red clover
Lotus corniculatus L.	Bird's foot trefoil
Ranunculus repens L.	Creeping buttercup
Viola lutea Huds.	Mountain pansy
Sagina procumbens L.	Procumbent pearlwort
Cerastium vulgatum L.	Mouse-ear chickweed
Potentilla erecta Hampe	Tormentil
Conopodium denudatum Koch.	Pignut
Galium saxatile L.	Heath bedstraw
Bellis perennis L.	Daisy
Achillea Millefolium L.	Yarrow
Leontodon hispidus L.	Common hawkbit
Taraxacum officinale Weber	Dandelion
Hieracium Pilosella L.	Mouse-ear hawkweed
Campanula rotundifolia L.	Harebell
Vaccinium Myrtillus L.	Bilberry
Calluna vulgaris Hull.	Ling heather
Veronica officinalis L.	Common speedwell
Euphrasia officinalis L.	Eye-bright
Plantago major L.	Greater plantain
P. lanceolata L.	Ribgrass
Rumex Acetosella L.	Sheep's sorrel
Juncus squarrosus L.	Heathrush
Luzula campestris D.C.	Field woodrush
Scirpus caespitosus L.	Tufted scirpus
Carex sp.	Sedges

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REPORT OF THE PERCY SLADEN EXPEDITION TO LAKE HULEH: A CONTRIBUTION TO THE STUDY OF THE FRESH WATERS OF PALESTINE

THE PLANT ECOLOGY OF THE DISTRICT

By R. FORBES JONES

(*With Plates* 18 *and* 19 *and three Figures in the Text*)

INTRODUCTION

It is only within comparatively recent years that there has been an intensive study of the biology of Palestine. A comprehensive survey of the flora and fauna was made by Tristram (1884), but more recent reviews are given in Bodenheimer's *Animal Life in Palestine* (1935) and in Post's *Flora of Syria, Palestine and Sinai* (1933). There are also certain publications in Hebrew from the Hebrew University at Jerusalem, but these are not easily available at the present time. Reference may also be made to the work of Dr Eig of that University, whose studies in the botanical field will ultimately serve to elucidate many of the floristic problems of Palestine.

In regard to the Lake Huleh district, however, investigation has been curtailed and fragmentary. Previously, this was due to the inaccessibility of the district and also to the interest being diverted to the more apparently interesting regions such as the Dead Sea Valley, etc. In more recent years also, when scientific work in Palestine has been greatly stimulated, the tension which has for a decade existed between the Arab and Jewish peoples has rendered it inadvisable to visit exposed regions such as the Huleh district unless in the short times of civil peace.

While the hydrophytic flora of other parts of Palestine has been more carefully studied, that of Lake Huleh has received rather less attention. Associated as this area is with the almost unique valley of the Jordan, and in view of the fact that a Jewish Land Development organization had acquired the rights of the lake and swamp and were, in 1935, preparing plans for the drainage and canalization of the whole area, the need was urgent for a record of the plants of this interesting district before complete loss of the aquatic flora occurred. Consequently, in July 1935, an expedition, with a personnel of two (Mr R. Washbourn as zoologist and the present writer as botanist), was sent out by the Trustees of the Percy Sladen Memorial Fund. The Expedition stayed throughout the hot summer months and until the end of December of the same year, when the heavy rains made further work impossible.

In a previous publication (Washbourn & Jones, 1938), the early historical references to Lake Huleh have been mentioned, and it would appear that at various times the lake has been almost completely dried up. Although the earlier travellers made little reference to the flora of the district, MacGregor (1886) described some interesting features of the reed swamp adjacent to the lake. A more general account of the flora and fauna has been made by Washbourn & Jones (1936).

AIMS AND METHODS OF THE EXPEDITION

The Expedition was stationed at the Malaria Research Laboratory of the University of Jerusalem, in Rosh Pinna, a village on the hills bounding the west side of the valley. Journeys to the lake and swamp were made every day except when the necessary sorting and preserving of material was to be done. Work on the lake was operated from Yesud ham Ma'ala, at which village boats were available.

The whole area of the lake and swamp (about 36 sq. km.) was somewhat too extensive to be completely studied during the stay of the Expedition with such a limited personnel. Especially was this so in the large swamp where the means of travel was chiefly by reed rafts, an extremely slow and tedious procedure. Some navigable channels had been cut through the *Papyrus* by the local fellahin at Mallaha and Jahula, villages on the malaria-infested edge of the swamp. These villages made convenient bases from which to make excursions into the swamp.

Some areas of the swamp have been left unexplored, e.g. the north-east side of the swamp. This area was difficult to reach during one day's journey; furthermore, the District Commissioner warned the Expedition against visiting this eastern area owing to some local trouble with the Bedouin. Ecological notes of the swamp were therefore taken from its more accessible parts, viz. the south-east area, the west and north-west areas, and in the vicinity of the River Jordan and the lake. It was possible, however, to make a more detailed study of the lake.

The plants collected were provisionally identified where this was possible and use has been made of the Herbarium of the Hebrew University, Jerusalem. Oxygen estimations were made of the water of the swamp and lake with a view to completing a chemical study of the two habitats. The estimations were done by Alsterberg's (1926) modification of the Winkler method. A B.D.H. Comparator was employed for measuring the *p*H values of the water and some water samples were brought back for chemical analysis.

THE HULEH DISTRICT

Lake Huleh (Pl. 18, phot. 1) is situated on the river Jordan in the region of Upper Galilee, and is the most northern of the series of three lakes[1] in the

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[1] Lake Huleh, Lake Tiberias (Sea of Galilee), and the Dead Sea, the latter being the most southern of the series.

Jordan Valley system. The lake and its adjacent swamp (Fig. 1) together form a lateral extension of the river Jordan and lie in the broad Huleh plain. This plain is bounded along the east side by a range of Syrian hills, on the north by Mount Hermon and its foothills, and on the west side by the mountains of Upper Galilee, which separate the valley from the Mediterranean Sea. The geological nature of the latter is like most of the mountains of Palestine in that there is an overlayering of limestone; the hills bounding the east of the plain, however, have an additional, superficial stratum of basalt.

The three main sources of the Jordan are in Mount Hermon and other Syrian mountains to the north, and the resulting streams from these flow down into the Huleh plain where they unite to form the river Jordan proper. The river then continues to flow southwards and soon enters the Huleh swamp through which it takes a well-defined course at present. But local tradition has it that the river changes its course at intervals.

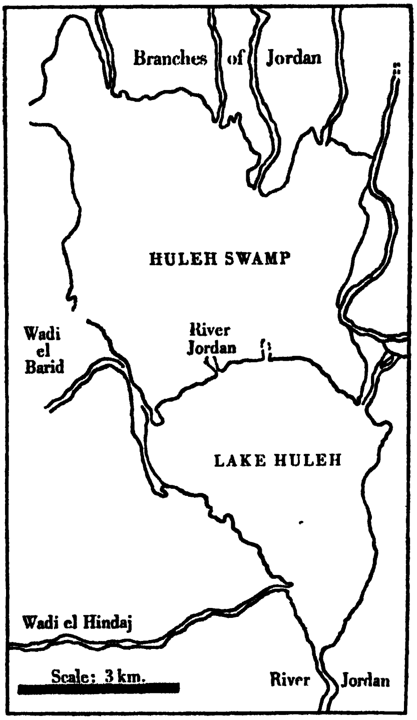

Fig. 1. A sketch-map of Lake Huleh and Huleh swamp.

After passing through the swamp, the river and derivative branches flow directly into the lake, which is contiguous with the swamp. This northern extremity of the lake is the broad end of a pear-shaped stretch of water, the narrow end being in the extreme south. To the south of the lake the Huleh valley ends in a low range of hills lying east-west, and it is through a narrow gorge in this range that the Jordan, after leaving the lake from its southern extremity, flows southwards to Lake Tiberias. Lake Huleh is approximately at the level of the Mediterranean Sea, while Lake Tiberias, some 16 km. to the south, is 205 m. below the Mediterranean sea level.

The level of Lake Huleh is apparently maintained by a large deposition of boulders and gravel, at one time brought down from the surrounding hills, at this southern exit of the Jordan, forming thus a lip over which the excess water of the lake constantly escapes. The present plan of drainage involves the removal of this "hump" so that the level of free water would fall.

Physiographical features of the district

There are, broadly speaking, only two seasons in the Huleh plain - the dry season which is also the hot season, and the rainy season, which is also the cold season. The dry season extends from June to October during which period there is generally no rainfall whatsoever. The temperature during this period often reaches a maximum in August when temperatures of 26–36° C. in the shade may be maintained and sometimes exceeded. The wind in the summer months tends to come from a south to west direction, while the winter winds more commonly originate in a north to east direction from the lake. After September or October, periodic showers of rain come with more and more frequency and intensity until about December or January, after which there is a gradual reduction in the rainfall until March or April. January is the coldest month, but temperatures below freezing are rare. There is very little precipitation in May, and with the advent of high temperatures the hot, dry summer begins.

Heavy rain is not continuous during the winter, when, in fact, long dry spells may intervene. Although the average annual precipitation on the western hills of the valley may be low, the amount of rain which may fall in a storm of short duration is tremendous. At such times the wadis carry a large volume of water into the valley, while the Jordan becomes swollen and overflows the shallow banks. The Jordan remains in flood practically throughout the winter, due, no doubt, to the rain and snow storms on Mount Hermon.

During the winter, therefore, the lake and swamp, which occupy the shallow basin of the valley, receive an immense volume of water; and since only a restricted volume of water can find exit through the narrow gorge in the south, the level of the water of the lake and swamp rises. During the summer, when the supply of water to the lake is decreased, the water level falls. This fall is accentuated by the great loss in evaporation from the lake and in transpiration by the swamp plants. It was learned from an authoritative source that the difference between this summer level of the lake, and the maximum winter level, is about 1 m. The water's edge of the lake and part of the swamp may recede 10–20 m., but where the slope of the ground surface is more gradual, the recession may be 50–200 m. or more.

The area of the lake and swamp is therefore subject to an annual tidal effect, and this naturally has a very definite effect on the shore limits of the aquatic and swamp flora. The majority of subaerial plants in Palestine develop during the rainy season when water is plentiful. Consequently, only those perennials which can withstand a period of immersion and can flower when the water level falls, and those annuals whose seeds can germinate in the lower damp areas and are able to survive the summer heat, are to be found in the lower littoral zone in the summer season.

With the aquatic and swamp flora, on the other hand, growth takes place when the temperature of the water and of the soil become propitious. These optimum conditions in the Huleh basin occur in the summer when the water level has receded nearly to its minimum, and this level would therefore determine the limits of the aquatic and swamp flora.

The lake

The lake occupies a shallow basin in the southern part of the plain, at the base of the eastern hills and about ½–1 km. or more from the western range. At its widest it is about 4½ km. broad east-west, and 5½ km. long north-south.

The average depth of the water is about 1½ m., but a few areas near the centre reach about 3 m. The slope of the bottom is very gradual towards the centre, and it is often possible to wade out considerable distances.

The wind direction and force over the Lake Huleh district must depend a great deal on local conditions, as for instance the rapid cooling of the night air round the summit of Mount Hermon and the flow of this cold air down into the warm valley beneath. Generally speaking, however, while no continuous critical observations were made, the light summer winds tend to come from the west to south-west. But in winter strong winds may suddenly spring up from a north to north-easterly direction. If wind action has any bearing on the deposition of silt this north to north-easterly *winter* wind will be of importance, as it is only in the winter that a great amount of silt is brought down by the Jordan and other wadis.

The lake bottom is generally of a characteristic brownish or greyish mud formed by the deposition of silt, but some variations of this occur. For instance, along the north side of the lake, parallel to the southern boundary of the swamp and stretching from the west to within a kilometre or so of the eastern shore there is a deposit of mud and plant debris. This mud bar may be within ½ m. of the surface and in some parts, e.g. at the mouth of the Jordan, it is almost exposed in the summer. This deposit is probably brought down mainly by the Jordan and the Wadi el Barid, since it is most noticeable where these enter the lake. A certain amount may also be brought down by a flow of water through the breadth of the swamp.

In the north-east corner of the lake, where the Wadi Darbashiya enters, the lake bottom is of a gravelly nature. This delta of the wadi is composed of old mollusc shells and shell gravel, together with the basaltic gravel brought there by the wadi and a little partially decomposed organic matter. A similar condition exists practically right down the eastern side of the lake, where the shore may also be composed of numbers of basaltic boulders and gravel, etc.

The western shore-line, on the other hand, reflects the geological nature of the western range of hills. The level of the western plain, with its alluvial soil and limestone boulders, gradually slopes from the base of the hills to the lake. At the lake side there is a more or less sudden fall of 2 or 3 m. to the beach. This beach may vary in breadth and slope, but its main feature is the large quantity of limestone pebbles mixed with shell gravel. The limestone pebbles of this west shore do not extend far into the lake before they become covered with mud.

The water of the lake, even in the summer, is coloured and rather opaque.

In the winter this may be largely due to fine brown silt suspended in the water. In the summer, when the clarity of the Jordan water and of the wadis shows that very little silt is being brought down, the brownish green, opaque appearance of the water is almost entirely due to a rich phytoplankton flora.

The day temperature of the lake varied on the location of the temperature station, e.g. in shallow or deep water, but where the conditions were similar it was found that very little difference occurred. Although the day temperature in the shallow water might approach the air temperature, the average temperature of the lake must be considered to be much lower than that. Table 1 shows some of the temperatures recorded.

Table 1. 24 *September* 1935. *Temperature of lake at different stations. Temperatures taken between* 11 *a.m. and* 12 *noon, local time*

	Temperature in °C.			
Station no.	Surface	Middle	Bottom	Depth m.
H 1 (*a*)	24·75	24·25	23·00	1·3
H 1 (*b*)	25·50	24·50	23·50	2·0
H 1 (*c*)	25·00	23·50	23·00	2·2
H 1 (*d*)	25·90	24·00	22·70	2·2

It is usual, as in Table 1, for the temperature of the lake bottom to be only a few degrees below that of the superficial layers, and for this difference to be gradual, so that there is no sharp distinction between a warm epilimnion and a cool hypolimnion as is sometimes found in deeper lakes.

In special locations in the lake one may find a more definite difference between the upper and lower layers, but this is due to submerged springs. Similarly, where the cooler water of the Jordan enters the lake, differences of 8° C. may be found.

As would be expected, in the colder seasons the day temperature of the lake becomes much lower and in November or December this may be in the region 16° C. Presumably, still lower temperatures occur in the coldest months of January and February. The vast volume of cold water brought down by the river Jordan and by the wadis will greatly accentuate this lowering of the temperature in the winter. A table showing comparative air and water temperatures about the lake during the stay of the Expedition has been given in a previous paper (Washbourn & Jones, 1938).

The water of the lake was of medium hardness and definitely alkaline. The analyses of the lake waters in Table 2 were performed by Messrs Rideal, Rideal and Scriver, London.

The organic matter would appear to be somewhat high, but this is consistent with the presence of the large amount of phytoplankton and with the circumstance of the main supply of water to the lake passing through the swamp vegetation.

Table 2. *Analyses of waters. Results expressed in parts per* 100,000

	Lake water 15. x. 35	Swamp channel water 31. x. 35
Suspended solids	Minute traces	
Dissolved solids	23·4	27·0
Chloride (as Cl_2)	1·5	2·0
Free ammonia	0·006	0·045
Albuminoid ammonia	0·018	0·03
Nitrate (as N_2)	Nil	Nil
Nitrite	Very faint trace	
O_2 consumed by permanganate (4 hr. at 80° F.)	0·528	0·488
*p*H value	7·9	7·3
Temporary hardness	11·09	16·13
Permanent hardness	3·77	2·47

Some estimations of the oxygen content of the water of the lake were made and these were shown to be, on the whole, normal. The estimations were made to provide relative data in a study of the habitats of the lake and swamp. It will be noted from these tables (Tables 3–5) that the oxygen content of the swamp is, on an average, about one-sixth that of the lake water. This would naturally be expected in view of the large amount of respiring roots, etc. (*q.v.*), in contact with the swamp water. The estimations were made by the macro-Winkler method as modified by Alsterberg (1926).

Vegetation on the shore and lake

The shore

In view of the "tidal" effect referred to, a description of the shore vegetation must include that area between the low summer level of the lake and (approximately) the high winter level.

A most obvious feature of this area is the zone of *Cynodon dactylon* (L.) Pers. which extends practically all along the shore on both the east and west sides of the lake. The upper limit of the zone seems to mark, approximately, the height to which the water-level rises during the heavy rains of January and February. Associated with the *C. dactylon* one often finds *Cyperus longus* L. and (in the vicinity of wadis and marshy places) *Panicum repens* L., *Echinochloa crusgalli* (L.) Beauv., *Eclipta alba* L., *Lippia nodiflora* (L.) Rich., and a few other moisture-loving plants.

The *Cynodon* community is more obvious on the east side of the lake where it forms an almost continuous closed mat some 8–20 m. broad. It is succeeded by the vegetation of the hillside which, during the summer months, consists of the dried, scorched stalks of the previous springtime vegetation. But where, as is characteristic on this eastern side, the wadis split fanwise, far up the hillside, into several smaller streams which flow directly down into the lake, the grass zone may be succeeded, between the arms of the wadis, by a dense vegetation which is dependent on this proximity to water. In such localities *Arundo donax* L. may be a locally dominant species as may other species, but some wadis have a vegetation in which *Vitex agnus-castus* L., *Nerium oleander* L., *Ricinus communis* L., *Rubus ulmifolius* Schott., are shrubs which occur together frequently, together with the occasional to frequent occurrence of such species as *Dianthus strictus* Banks & Soland., *Erythraea spicata* (L.) Pers., *Pulicaria vulgaris* Gaertn., *Verbascum sinuatum* L., and *Verbena officinalis* L., etc.

On the west side, as opposed to the east, the grass zone may either be non-existent, or grow in open or closed formation; it may be present as a narrow fringe about a metre wide, or in some parts only it may be several metres wide. The extent of the zone is certainly correlated with the nature and slope of the beach. There is better opportunity on this west side to observe a zonation of the vegetation which seems to be governed by height above the water table, summer or winter levels.

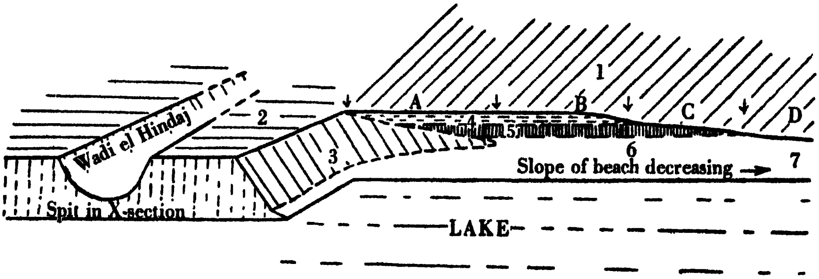

Fig. 2. A diagrammatic representation of the zonation of plant communities on the shore near the Wadi el Hindaj. 1, cultivated ground; 2, *Alhagi maurorum-Prosopis farcata* community; 3, *Vitex agnus-castus* community; 4, *Centaurea calcitrapoides* community; 5, *Alhagi maurorum* community; 6, *Cynodon dactylon* community; 7, damp, more level area, where moisture-loving plants appear. As the top of the beach falls from *A* to *D* there is a gradual loss of the upper zones. The *Vitex* disappears as the distance from the wadi increases.

Such a vertical zonation is very clearly demonstrated near Yesud ham Ma'ala (Fig. 2). In the higher limits the *Cynodon* community generally yields dominance to an *Alhagi maurorum* Boiss. community where the species *Centaurea carduiformis* DC., *Scolymus hispanicus* L., *Sinapis incana* L. and *Torilis neglecta* R. & S. are occasional. The *Alhagi maurorum* is generally infested with *Cuscuta monogyna* Vahl. or *C. pedicellata* Ledeb.

Within a few metres this last-named community is replaced by one in which the dominant species is *Centaurea calcitrapoides* L., although *Rubus ulmifolius* may show local dominance. *Lactuca scariola* L. and *Plumbago europaea* L. are occasional species in this higher zone.

Near the Wadi el Hindaj the species *Vitex agnus-castus* occupies a position between the *Cynodon* and the *Alhagi* communities (Pl. 18, phot. 2).

The steep sides of the spit formed by the Wadi el Hindaj are occupied by a narrow fringe of *Cynodon* close to the lake edge, followed by a zone of *Vitex*, while on top of the broad spit *Prosopis farcata* (Banks & Soland) Eig is locally dominant or co-dominant with *Alhagi maurorum*. On the open stony ground of this area *Heliotropium villosum* Willd., *Plantago lagopus* L., *Paronychia argentea* Lam. and *Ammi visnaga* (L.) Lam. are frequent, while *Hedypnois cretica* (L.) Dum-Cours and *Chenopodium album* L. are occasional. The actual banks of the wadi running through the middle of the spit are a dense growth of *Vitex*, a species generally only found in such habitats in the near vicinity of wadis.

The flora in the dry bed of this wadi is very sparse, but the delta which is exposed during the summer low level of the lake is much more successfully colonized. Actually in the bed of the wadi some of the more characteristic species are *Amaranthus chlorostachys* Willd., *Heleochloa schenoides* (L.) Host., *Glinus lotoides* L., *Hemarthria altissima* (Poir.) Stapf. & Hubbard, etc., but on the delta there is a relatively frequent occurrence of young specimens of *Vitex* and *Solanum nigrum* L., and such species as *Amaranthus sylvestris* var. *graecizans* (L.) Boiss., *Sonchus oleraceus* L., *Erodium malacoides* (L.) Willd. are occasional.

The littoral zone.

By the littoral zone is meant that damp fringe along the water's edge when the lake is at its summer low level. This is very sparsely colonized and the vegetation grows on the patches of moist or wet mud between the boulders and stones. Some of the species typical of those areas more suitable for supporting vegetation are: *Alternanthera sessilis* (L.) R.Br., *Cyperus flavescens* L., *C. fuscus* L., *Fimbristylis bis-umbellata* (Forsk.) Bub., *Spirodela polyrhiza* (L.) Schleid., etc.

The springs.

Mention may here be made to those springs occurring near to the lake and swamp. The two most notable are on the west side at Mallaha and at Jahula; there are also the "sulphur" springs at El Almaniya. It is only at such springs as the former that there occurs under the shading boulders or in caves, the fern *Adiantum capillus-veneris* L. The cave at Jahula is also one of the few places near the lake and swamp where mosses are to be found in the summer.

The "sulphur" springs arise in little pools through which sulphurous gases are seen to bubble. These gases may have been formed under the lake or swamp, to be forced out, or to come out of a solution saturated under pressure, through these springs at Almaniya. The flora in the pools and the streams from these consists of algae, and these were, of course, collected.

The lake.

The distribution of the flora of the lake does not seem to bear any relation to depth of water except in so far as this may determine the shore limits of any of the communities. It is probable that the factors determining the distribution are (*a*) rate of silting and/or (*b*) the nature of the silt (Pearsall, 1920). Apart from the algae on stones and a few isolated patches of *Vallisneria spiralis* L., there is generally little submerged vegetation within 10–50 m. from the water's edge. However, almost the whole lake bottom is covered with a vigorously growing mass of vegetation.

A vegetation map of the lake (Fig. 3) was made by plotting the results of a series of transects from the Yesud ham Ma'ala base. The approximate relative positions of the various communities are shown in the map, but it must not be supposed that the lines of demarcation between them are as clear as indicated; the transitions are usually more or less gradual. The positions of occasional small colonies are not shown in the map as this would tend to obscure the otherwise very definite distribution of the major communities.

The main communities to be found in the lake are those dominated by (1) *Myriophyllum spicatum* L., (2) *Myriophyllum spicatum* and *Potamogeton lucens* L., (3) *Nuphar luteum* (L.) Sibth. & Sm., (4) *Vallisneria spiralis* L. and *Naias marina* L., (5) *Potamogeton pectinatus* L., (6) *Potamogeton nodosus* Poir., (7) *Ceratophyllum demersum* L. and (8) *Phragmites communis* Trin.

(1) *The* Myriophyllum spicatum *community.* This community occupies the greater area of the southern half of the lake where it is pure for the species and is growing on the typically light brown-grey mud. At the limits of distribution the *Myriophyllum* may become co-dominant with other species, as, for instance, in the north-west limit of the community where the species becomes co-dominant with *Potamogeton lucens* forming

(2) *The* Myriophyllum spicatum-Potamogeton lucens *community.* Stretching northwards this community becomes lost in the *Nuphar* community. There are a few areas near the south-east shore where the *Potamogeton* forms small communities by itself.

(3) *The* Nuphar *community.* While small communities of this species are to be found in many sheltered corners of the lake, its most extensive development is reached in the northern half of the lake. The *Nuphar* plants grow most dense next to the swamp and in the region of the mud bar which has been noted; southwards towards the deeper waters, growth becomes less extensive, and the surface of the water is not such a dense mass of leaves as is to be found in the more northern area (Pl. 18, phot. 4). In most of the northern area of the community, the *Nuphar* is dominant but *Ceratophyllum demersum* is frequent, as also—in some parts—is *Myriophyllum.* Little colonies of *Ranunculus aquatilis* L. are found locally near the mouth of the Jordan where the mud bar is near the surface. The *Nuphar* community may also be interrupted by "islands" of *Phragmites communis*, *Cyperus papyrus* or *Typha angustata.*

(4) *The* Vallisneria spiralis-Naias marina *community.* This community is very conservative and is practically confined to the north-east corner of the lake where the Wadi Darbashiya enters. The substratum here is obviously different from most of the rest of the lake and is principally composed of shells and shell and basaltic gravel mixed with some partially decomposed organic

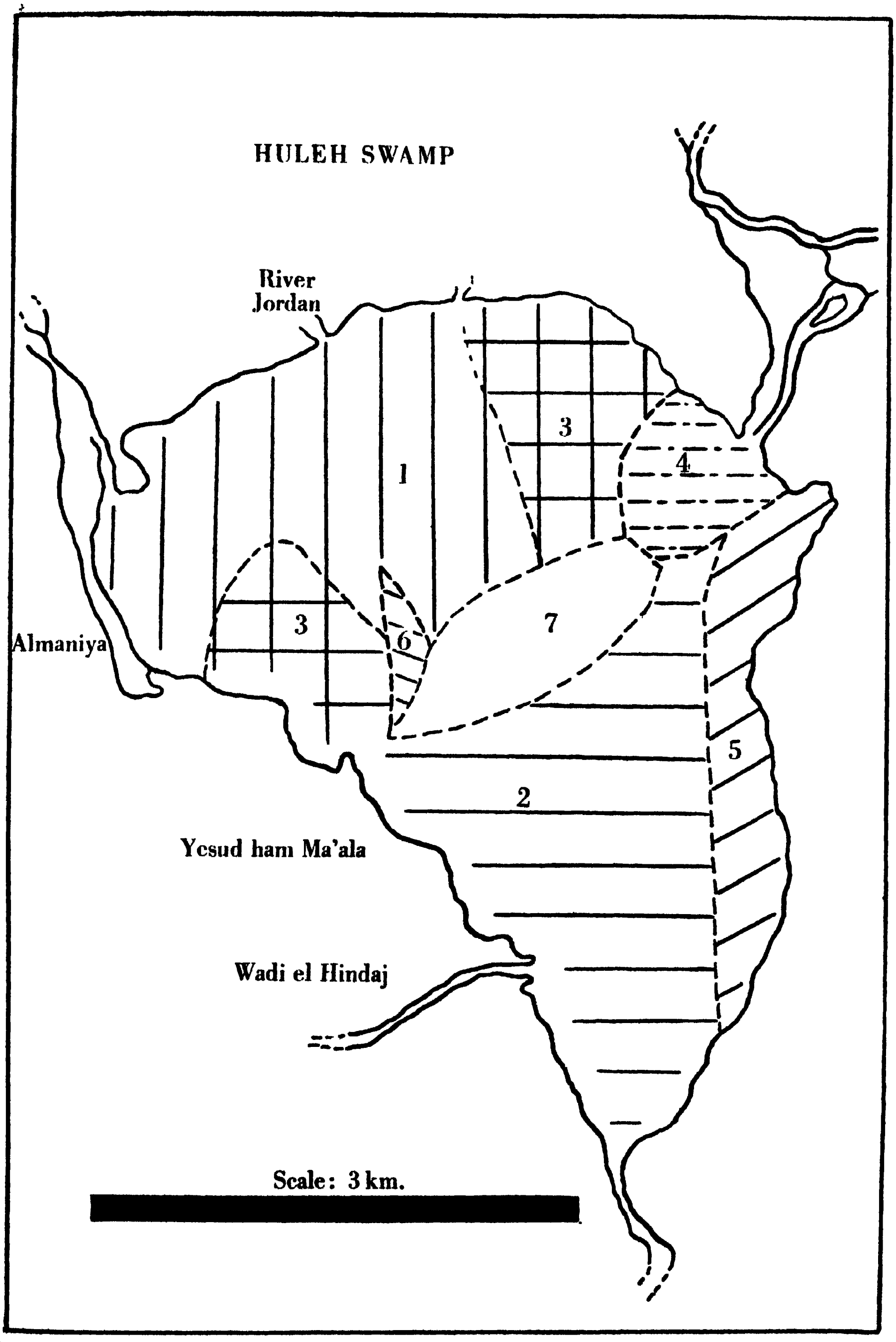

Fig. 3. A diagrammatic representation of the positions of the various plant communities of the lake. 1, *Nuphar luteum* community; 2, *Myriophyllum spicatum* community; 3, *Myriophyllum-Nuphar* community; 4, *Vallisneria spiralis-Naias marina* community; 5, *Potamogeton pectinatus* community; 6, *Myriophyllum-Potamogeton lucens* community; 7, an area devoid of vegetation; no reason can be given for this.

debris and some mud. Only the *Vallisneria* is to be found far away from this area, and it is then found where coarse gravel has been deposited.

(5) *The* Potamogeton pectinatus *community*. Except for occasional plants in other parts of the lake, this species is absolutely confined to the east side as a community some 40–50 m. from the shore and about 3 km. long. It approaches the shore to where the water is about ½ m. in depth and maintains dominance to a depth of 1·2 m. or so, where it gradually becomes replaced by the *Myriophyllum* community.

(6) *The* Potamogeton nodosus *community*. As would be expected, this species occurs in its customary habitat in the shallower waters and is found at various points around the lake but notably at the mouths of some of the wadis.

(7) *The* Ceratophyllum demersum *community*. While *Ceratophyllum* occurs frequently, especially on the north side of the lake among the *Nuphar*, it becomes the dominant species in only one area at Almaniya, on the west side of the lake. Here the community occupies an area of about 1500 sq. m. or more, and is in a position between the *Nuphar* and the *Phragmites*. The plants are growing in such quantity that it is very difficult to walk through them. Probably it has succeeded the *Nuphar* since the substratum contains old and decaying rhizomes of *Nuphar* under the silt. In some of the shallower parts and where the *Ceratophyllum* is less dense, occasional specimens of *Chara vulgaris* L. and *Nitellopsis obtusa* J. Groves are found.

(8) *The* Phragmites communis *community*. Silted areas along the shore support *Phragmites*; such is the case along the east and south sides of the lake and more especially on the west side where there is a continuous stretch of *Phragmites* from El Almaniya (Pl. 18, phot. 3) to as far north as the swamp. Indeed, this zone, with little interruption, is continuous on this west side right up to the north of the swamp. In the lake the zone is about 50 m. wide and extends, in the summer, from the water's edge to a depth of about 1 m. The only other species to be occasionally found in the *Phragmites* zone are *Sparganium erectum* L. and *Lycopus europaeus* L., these occurring where the black mud is incompletely covered with water.

Cultivation is carried on right up to the *Phragmites* community at Almaniya, and owing to the configuration of the land the adjacent field is flooded by the first rains. A few small mounds are left unploughed, however, and on these the only few specimens of *Datura stramonium* L. to be found were growing. In the water of the lake near this area was found a specimen of *Scirpus littoralis* Schrad.

THE SWAMP (ARD EL HULEH)

The large swamp to the north of the lake covers an area of over 22 sq. km. This is almost completely a dense jungle of vegetation, but a comparatively few areas of open water occur, e.g. the cuttings formed by the Jordan, etc., certain narrow waterways cut open by the Arab fellahin for purposes of travel, and a few open pools or clearings of various extent which may be found in different parts.

In the pools of still water the temperatures are similar to those of the lake, but in the channels and waterways the temperatures may be a few degrees lower. In addition, the daily range of temperature in the channels is lower than that of the pools or lake. No doubt this is due to the flow of cool water along the channels, this probably being derived from springs or from offshoots of the Jordan, or both.

The subnormal oxygen content of the swamp water might be correlated with the sources of the water and with the amount of decaying debris and of respiring roots in contact with it. Some oxygen estimations are given in Tables 3, 4 and 5.

Table 3. 3 *November* 1935. *Oxygen content of some of the habitats*

Habitat	ml. O_2/litre at N.T.P.
Swamp: (*a*) in channel	1·086
(*b*) among vegetation	1·212
Pool at Ain el Mallaha	5·241
Lake at El Almaniya	6·368

Table 4. 7 *November* 1935. *Oxygen content of some of the habitats*

Habitat	ml. O_2/litre at N.T.P.
Channel water	0·814
	0·839
Phragmites at El Almaniya	1·055
	1·023

Table 5. *Comparison of habitats on same day*

Habitat	ml. O_2/litre at N.T.P.
Papyrus swamp: (*a*) in channel	1·065
(*b*) among vegetation	0·834
Phragmites at El Almaniya: (*a*) inner	1·86
(*b*) outer (i.e. next to lake)	6·317
Lake	6·296

There is also a difference in the chemical properties of the lake and swamp water. The analysis is given in Table 2, and it shows that this channel water is a little harder than the lake water. It is also less alkaline, a fact which may be associated with the close contact of the channel water with the organic debris of the swamp. It is important to note that it is always neutral to alkaline, as this probably has a particular effect on the peat formation in the swamp (*q.v.*).

Vegetation of the swamp

The vegetation of the swamp can be divided into two main categories: (*a*) the fringing reed swamp which is mainly composed of sedges and reeds, and (*b*) the main *Papyrus* swamp. In addition to being a useful division of the swamp vegetation for purposes of description, this general division probably also represents two distinct developmental series which are independent of one another and are of separate, unrelated origins.

(*a*) *The fringing reed swamp.*

This reaches its greatest development on the western periphery of the *Papyrus* swamp, and the following description is based on observations on this western side. It forms a "fringe" along the main body of the *Papyrus* swamp, the innermost *Phragmites* community of the fringe and the *Papyrus* abutting directly on one another.

This community of *Phragmites* is a constant feature of this western side and generally occupies the deeper waters. Nearer the shore, in about 30 cm. of water, there is a zone of *Typha angustata* Bory & Chaub., several metres broad, and this also is a more or less constant feature. In shallower waters communities dominated either by *Cyperus serotinus* Rottb. or *Sparganium erectum* L. are observed, and these are followed by a broad zone of *Cynodon dactylon*, 20–30 m. or more wide and terminating in cultivated ground (Pl. 19, phot. 6). Occasionally the *Cynodon* community is separated from the swamp by an intervening community of *Jussiaea repens* L. growing in marshy ground.

In the *Cyperus* or *Sparganium* zone at the edge there is an occasional to frequent occurrence of *Butomus umbellatus* L., *Mentha aquatica* L., *Cyperus alopecuroides* Rottb., etc.; in the *Typha* community *Scirpus lacustris* L. is locally co-dominant. Other species found occasionally are *Hydrocharis morsus-ranae* L., *Alisma plantago-aquatica* L., *Juncus fontanesii* Gay ex Laharpe, *Nitella oligospora* Br., etc.; and the interesting species *Marsilea diffusa* Lepr. ex A.Br. is frequent in one small area only. In the *Phragmites* community *Lythrum salicaria* var. *tomentosum* DC. is occasionally found, and the twiner *Cynanchum acutum* L. is also in evidence.

On the east side of the swamp the fringing reed swamp may be absent, or, on the other hand, some of the communities typical of the western side may be absent. Near the south-east side, for instance, there are a few large stretches of open water (Pl. 19, phot. 8). The inner sides of these are generally bounded by *Papyrus* while the outer may lead through a *Jussiaea repens* community to the *Cynodon* zone. A dense community of *Sparganium erectum* may take the place of the *Jussiaea*. In other parts of the east side, however, there may occur a restricted fringing reed swamp in that the shallow water of the edge may support a community of *Sparganium*, for instance, this being followed by a *Typha* community abutting directly on the *Papyrus* swamp; the *Phragmites* zone is often missing.

There seems to be a more widespread tearing up of *Papyrus* roots on this eastern side for fuel, and this may partially account for the confusion of the vegetation; here, as very often, the open stretches of water have obviously within recent time been covered with *Papyrus*. At the same time, there seems no doubt that the developmental history of the vegetation in this area has its reflexion in the present-day distribution (cf. Discussion).

On the north side there is also some confusion in the vegetation as a result of elementary forms of land reclamation carried out by the Arab fellahin for agricultural purposes. In the most recently drained land maize and millet are sown between the old rhizomes of *Papyrus*, without very much preliminary ploughing. In such places some typically swamp- and moisture-loving plants persist here and there, but no doubt these will in time disappear.

The southern extremity of the swamp abuts immediately on the lake. Generally there is a sharp line of demarcation between the lake and swamp, the tall mass of *Papyrus* ending abruptly. Towards the west of this south side, however, there are "islands" of vegetation. It would appear that these are formed by fragments of *Papyrus* breaking off from the main body of the swamp and floating outwards to come to rest on mud banks which come near the surface of the water. A fragment would grow out in all directions to form an island, treacherous to walk on, but held in place by the *Papyrus* roots. Other plants often find a resting place on these islands, and one often finds that the *Papyrus* has become co-dominant with *Typha angustata* and that the island has become fringed with *Jussiaea repens* (Pl. 19, phot. 7). Such an island, in expanding, would gradually grow outwards to the lake and also meet in another direction the advancing main body of the swamp. There is no doubt that the swamp is encroaching on the lake and that, in a natural course of events, it would only be a matter of time before the whole basin of the Huleh would be one large *Papyrus* swamp.

(*b*) *The* Papyrus *swamp.*

This constitutes the main body of the swamp proper and is mainly comprised of *Cyperus papyrus* L. Typically the *Papyrus* is growing in water ½–2 m. deep. In this habitat the thick rhizomes are so intermingled as to form a "raft" 10–30 cm. below the surface of the water, and this is usually strong enough to bear a man's weight without breaking. It is, however, extremely difficult to walk over, and each step causes a sinking and movement of the vegetation for several metres around.

Intermingled with the roots, which grow vertically downwards to the floor of the swamp, is a mass of old rhizomes, etc., of *Papyrus*, while the living rhizomes always keep more or less on top of this accumulated dead material. This mass of debris is continually increasing, but the neutral or alkaline nature of the water results in the formation of a mild form of peat. Obviously, as this consolidation to peat continues, the floor of the swamp is gradually raised. Indeed, during the summer months one can find the many stages between the condition of a loosely-bound, submerged debris and one where the peat has become exposed above the water table; in many such instances the water table may be ½–1 m. beneath the surface of the peat. The *Papyrus* is found to continue to grow on this exposed peat and is apparently as healthy as when growing in the more aquatic habitat (Pl. 19, phot. 5). With the advent of the rainy season when, as has been mentioned, the water level may be raised 1 m. or so, this exposed peat would become reinundated. This periodic immersion of mild peat with alkaline water is reminiscent of the fen type of habitat.

Tests with a B.D.H. Comparator show that the *Papyrus* peat is definitely alkaline, especially near the surface. The more obvious remains in the peat are of *Papyrus* and *Polygonum* spp. At the level of the water table, when this is some distance beneath the peat surface, there is evolved an obnoxious sulphurous odour.

In the "floating"[1] *Papyrus* community the number of species represented is small, although those which are present occur frequently. Most of the species found form a lower vegetation stratum shaded by the tall *Papyrus* (usually 4 or 5 m. high), but one or two of the taller species are able to reach the more direct light. The plants all grow in little accumulations of organic material which have come to be held by the matted rhizomes of the *Papyrus*.

The most characteristic species in the "floating" *Papyrus* community is *Dryopteris thelypteris* (L.) A. Gray, and this is frequent all over the *Papyrus* community. Other species which are occasional to frequent are *Lycopus europaeus* L., *Lythrum salicaria* var. *tomentosum* DC., *Polygonum lapathifolium* L., *P. scabrum* Poir., etc. These species are found to a similar extent on the "dry" *Papyrus* swamp areas, but where the *Papyrus* has been cut down and clearings have been made many moisture-loving plants make their appearance. In such places the growth is most luxuriant. Additional species which are locally frequent in this "dry" swamp are *Bidens tripartita* L., *Galium elongatum* Presl., *Hydrocotyle ranunculoides* L.f., *H. vulgaris* L., *Polygonum tomentosum* Willd., *Scutellaria galericulata* (L.) var. *pubescens* Benth.,[2] *Solanum nigrum* L., etc.

Occasionally in these open spaces one finds a species of *Salix* (*babylonica*?) growing on the peat. There are other areas of peat supporting communities of *Cladium mariscus* L., but it is uncertain whether the *Cladium* has naturally succeeded the *Papyrus* or if the *Papyrus* has previously been cut down and removed by the fellahin. Where the *Cladium* occurs, it is of extremely vigorous growth and the plants are of large size; the ground flora is very much reduced to occasional specimens of *Jussiaea repens*, *Solanum nigrum*, etc.

Some areas of the "dry" peat now support communities of *Phragmites* or of a mixture of this and *Papyrus*.

The artificial waterways which traverse the swamp are invariably fringed with *Ceratophyllum demersum* with, occasionally, the occurrence of *Utricularia vulgaris* L. The open pools may harbour species of *Polygonum*, *Nuphar luteum*, etc., but it is noteworthy that *Nymphaea alba* L. occurs only in the swamp.

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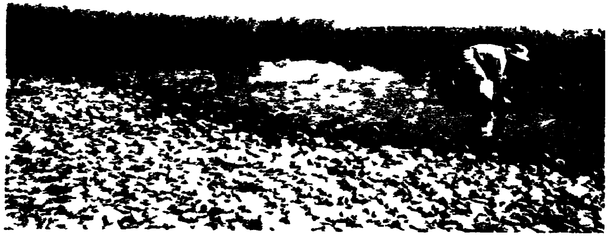
[1] Not strictly "floating", as the roots of the *Papyrus* reach the mud floor of the swamp.

[2] Critical identification by Dr Eig, Hebrew University, Jerusalem.

Phot. 1. Lake Huleh from the Syrian hills on the east of the valley, looking north.

Phot. 2. Beach near Yesud ham Maala with mat of *Cynodon dactylon* and shrubs of *Vitex agnus castus*.



Phot. 3. Southern limit of the western *Phragmites* and *Nuphar*. Black line on horizon is the main *Papyrus* swamp.

Phot. 4. The *Nuphar* community of the lake.

Phot. 5. The "dry" *Papyrus* swamp (about 4 m. high) with undergrowth of *Dryopteris thelypteris*, *Bidens tripartita*, etc.

Phot. 6. The edge of the swamp, with low sedges on the right, the grass zone and an *Inula viscosa-Juncus acutus* community on the left.

Phot. 7. Two "islands" of *Typha* and *Papyrus*, fringed with *Jussiaea repens* on the south of the swamp.

Phot. 8. Looking west (from S.E.) towards the main *Papyrus* swamp, with *Nuphar* and *Echinochloa crusgalli* in the foreground.

DISCUSSION

In regard to the distribution of the vegetation of the lake, it is certain that water depth is not the controlling factor. The distribution is probably more related to the differential rates of silting in the different parts of the lake and also to the variation in the chemical and physical nature of the silts (Pearsall, 1918, 1920). Silting will be greatest in the winter when the heavy flood rains occur, so that the factors having the greatest effect on silting will be those operating in the winter. Among such factors may be mentioned the winds which in winter come from a northern to easterly direction, and can on occasion produce considerable wave action. The silt brought down by the Jordan and by the Wadi el Barid would therefore be deposited in a differential manner southwards, but the winter winds would tend to cause a deflexion of the silting in a westerly direction, towards the large "bay" forming the Almaniya shoreline. It follows that least silting would occur on the eastern side of the lake, and it has been noted that the lake bottom in the north-east corner (especially) and along a part of the east shore is, in fact, of a gravelly nature.

On a basis of these general observations it would seem that the *Vallisneria* and the *Naias* are only able to survive where the rate of silting is relatively low while the *Nuphar* can occupy a position where the rate of silting is probably very high. *Potamogeton lucens*, *P. pectinatus* and *Myriophyllum spicatum* would thus occupy intermediate positions in regard to the rate of silting.

The relative rates of silting over the lake is also reflected in the distribution of *Phragmites*. The silting along the western shore must be moderate, and it is here that there is found a broad, continuous mass of *Phragmites*. Along the eastern shore, however, where the rate of silting is relatively low, the *Phragmites* occurs sporadically and the communities are small and separate and often stunted.

The *Papyrus* mass is continually growing forward over the free lake surface, and this fact in itself would gradually alter the features of silting. However, as the *Papyrus* mass advances over the lake, the submerged vegetation would ultimately disappear and the *Phragmites* of the lake shores would then become part of the fringing reed swamp. In such an eventuality, the *Phragmites* community of the west shore from Almaniya northwards would become a *continuous* zone along that edge of the swamp, while the eastern side of the more recently formed swamp would show sporadic appearance of a *Phragmites* zone along the periphery. Such a condition would be reminiscent of the present-day status of the *Phragmites* in the fringing reed swamp on the east and west sides, the clue to which will probably be found in the previous history of the localities when the *Papyrus* swamp was not so extensive as it is to-day, and when the free lake surface was of greater extent.

The *Papyrus* swamp and the fringing reed swamp are thus of distinct origin, the latter being formed in relation to silting and other factors in the lake, while the *Papyrus* swamp is formed by merely growing over and covering free lake surface. However, as the *Papyrus* mass embodies the *Phragmites* communities as a definite fringing zone, the presence of the *Papyrus* would cause an alteration, and probably a suspension, of silting in these newly incorporated areas. In this way the *Papyrus* swamp would be a factor in the determination of the final character of the fringing reed swamp. Observations indicate that the zonation previously described, from the *Cyperus serotinus* or *Sparganium erectum* in the shallow waters of the edge, then *Typha* in about 30 cm. of water and finally *Phragmites*, is not to be found anywhere but in the region of the swamp. It is unfortunate that biotic factors operate very strongly along the edge of many of the lake communities of *Phragmites*, but nevertheless there is no evidence of the zonation characteristic of the swamp area. There must also be significance in the fact that on the edge of the more recently formed swamp, viz. the south-west and south-east areas, there are in both cases considerable areas covered with *Sparganium erectum*. It is uncertain, however, to what extent the occurrence of these large areas of *Sparganium* are due to the previous operation of biotic factors such as the cutting down of reeds, etc.

In any area which has become covered by *Papyrus* there is a relatively rapid formation of peat. The surface of the peat is gradually raised above the water level until, in the summer, the water table may be 1 m. or so beneath the peat surface level. This peat has been formed under alkaline conditions (the water is alkaline) and is of a mild form having distinct neutral to alkaline reactions. At the same time, it may be recalled, the annual fluctuations of the water level causes the exposed peat to be periodically inundated with alkaline water. Such a condition is not unlike that found in fen habitats, and the *Papyrus* peat at Huleh may be considered a fen peat. It is thus not surprising that in certain areas *Cladium mariscus* has become the dominant species. However, the *Cladium* communities may represent a stage in deflected succession as it is possible that the *Papyrus* previously growing in these particular areas may have been cut down and the rhizomes removed for fuel, providing thus an opportunity for recolonization by other plants. There is a large *Cladium* community near the mouth of the Jordan and in this the *Cladium* is large-growing and dominant, while only a few specimens of other representatives of the swamp flora are to be found. Adjacent to this area, however, *Papyrus* has obviously been cut down and the newly exposed peat surface is now covered with a lush growth of herbaceous swamp plants. In another adjacent area, heaps of *Papyrus* rhizomes can be observed, having been collected by Arabs some time previously. Continuous observations would require to be made on such areas in order to elucidate the various problems of succession in the swamp.

Similarly, in some areas, *Phragmites* seems to have succeeded the *Papyrus*, but this may also represent deflected succession. However, in an area near Mallaha, *Papyrus* has "invaded" the *Phragmites* community so that at a rough computation, there is 25 % *Papyrus* and 75 % *Phragmites*. The *Papyrus* will certainly rapidly form peat so that there probably would emerge such a mixed community as may be observed adjacent to the above where there is 50 % *Papyrus* and *Phragmites* growing on *Papyrus* peat about 1 m. above the summer level of the water table. Obviously, if the whole were cut down, it would be very possible for the *Phragmites* completely to replace the *Papyrus*.

Generally speaking, it would appear that the swamp is not yet mature enough for there to be seen a natural succession from *Papyrus* as the normal close stand of the *Papyrus*, even on the deep peat, prevents this from drying up and causing such changes as to bring about a natural change in the vegetation. By cutting and by making clearings, the *Papyrus* can be replaced by a dense herbaceous growth which is probably a forerunner of the *Cladium* community. There is no direct evidence that *Phragmites* can naturally succeed *Papyrus* which can show great tenacity of life; or that *Phragmites* could compete with other plants for any cleared space unless the *Phragmites* was already there or was near enough to colonize by means of runners.

As a point of interest it may be observed that in the event of canalization of the swamp area, allowances will have to be made for what will almost certainly be a lowering of the peat surface by oxidation of the *Papyrus* peat, A parallel may be found in the sequence of events subsequent to the drainage of Wicken Fen in England.

ACKNOWLEDGEMENTS

Opportunity may here be taken to express thanks to the many people who assisted the Expedition in many valuable ways. We are indebted to the Trustees of the Percy Sladen Memorial Fund for financing the Expedition and to Dr and Mrs Mer of the Malaria Research Station, Rosh Pinna, for the many kindnesses they showed while the Expedition was in Palestine. Our thanks are also due to Prof. Bodenheimer and his staff at the Hebrew University at Jerusalem for the interest shown in the work of the Expedition; indebtedness is also expressed to Dr Eig of that University for permission to use, and for assistance in, the University Herbarium where many of the specimens were provisionally identified, although the responsibility for the final naming of the specimens rests entirely with the staff of the Botany Department of the British Museum, to whom appreciation is now shown. Our thanks are also due to Prof. W. Stiles, and Prof. H. Munro Fox, for giving us leave of absence from Birmingham University and for much help in other ways. Prof. J. Stanley Gardiner gave much valued advice to the Expedition as did many others; in particular may be mentioned Dr J. Ramsbottom, Dr G. S. Carter, Prof. P. A. Buxton, Prof. W. Leach and Prof. W. H. Pearsall. The present author is greatly indebted to Prof. Pearsall and Dr Ramsbottom. We further acknowledge the loan of apparatus from the Zoological Department, Cambridge, and the

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A VEGETATION MAP OF KENYA

WITH PARTICULAR REFERENCE TO GRASSLAND TYPES

By D. C. EDWARDS

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(*With Plates* 20 *and* 21 *and one Map*)

THE Colony and Protectorate of Kenya are situated in the east-central portion of Africa. The equator passes approximately through the centre, and the country extends to just over 4° north and a little beyond 4° south. The territory is occupied mainly by the colony; and the protectorate consists of a comparatively narrow coastal strip. The coastline, which is entirely within the protectorate, faces the Indian Ocean to the south-east. The country is bounded on the north by Abyssinia and the Anglo-Egyptian Sudan, on the west by the high-rainfall country of Uganda, on the south by Tanganyika Territory and on the east by the dry Italian Somaliland. The land area of Kenya is 219,730 square miles.

The rainfall of Kenya varies in a general way from extremely dry conditions to the north and east, where the rainfall is erratic and as low as 10 in. (*c.* 25 cm.) per annum or even lower, to the high moisture conditions of the region of Lake Victoria Nyanza with a rainfall of 60 to 80 in. (*c.* 150–200 cm.). This general trend of the moisture conditions is interrupted by the highland area which is situated in the central and western portion of the country. This elevated land mass lies mainly at altitudes of from 5000 to 6000 ft., although portions of the occupied area extend to over 9000 ft., and mountain peaks are included, which, in the case of Mount Kenya, attain a height of over 17,000 ft. These elevations naturally exert considerable influence in lowering the temperatures which would otherwise prevail and in producing comparatively high rainfall over considerable parts of the highland area. In the portion to the east of the Great Rift Valley, which cuts through the country roughly from north to south, the rain is derived mainly from the north-east monsoon, which blows from April to June and again in November, while the climate of the western portion is affected, in addition, by rain-bearing winds from Lake Victoria Nyanza. At the higher altitudes mountain mists are an important factor in the moisture conditions and probably have considerable bearing on the types of vegetation which exist in these localities.

It will be seen, then, that a very wide range of climate exists in Kenya. The greater part of the country to the north and east is arid and hot, towards the west there is a tendency for change to the moist, tropical conditions of the adjoining territory of Uganda, which conditions are approached in the Lake Victoria basin. The highland area, occupying approximately one-third of the country, has a climate which may be described as subtropical, except for the short duration of its equatorial days. Climatic islands of great ecological interest are a feature of the mountainous country.

The soils of Kenya are extremely variable and, over the greater part of the country, are only vaguely known. So far as they are known, they appear to show no very distinct relationship to the main vegetational types.

The vegetation is predominantly grassland, which occupies, in one or other of its forms, practically the whole country with the exception of portions of the higher mountain masses where forest is situated. The main types of vegetation are forest, mountain grassland, parkland or savannah and semi-arid grassland.

Forest, excluding the less important types of thorn forest and mangrove, occupies only a limited portion of the country, in the region of 6000 square miles. It is situated chiefly on the slopes of the main mountain masses of Kenya, Elgon, the Aberdare Range, the Kikuyu-Laikipia Escarpment and the Mau-Elgeyo-Cherangani mountain system. The mountain grassland occurs above the forest line at about 10,000 ft. altitude, and within the forest area and at its lower margin, chiefly where the forest vegetation has been suppressed by fire over considerable periods in the past. The parkland vegetation embraces the extensive acacia-tall grass savannah and the areas shown on the map as high moisture savannah. The acacia-tall grass savannah, which consists typically of scattered, flat-topped thorn trees in an even cover of tall grass, occurs chiefly as a belt encircling the highland zone and running into all the drier areas within the highlands. Between this vegetation and the vast arid areas to the north and east of the country occurs the acacia-desert grass savannah which is a modification of the acacia-tall grass type, but with the trees frequently much reduced in size and with an exceedingly sparse ground-cover of desert grasses. The high moisture savannah, which consists of broad-leafed, deciduous trees, either scattered or in distinct groups, in a plentiful cover of high (5–8 ft.) grasses, is confined mainly to the high-rainfall country towards Lake Victoria Nyanza. The greatest areas of this type occur in the Trans Nzoia, the Trans Mara and the Sotik areas. The remainder of Kenya to the north and east, apart from a coastal strip, consists of vast stretches of semi-desert, where the soil surface is, to a large extent, devoid of vegetation except for widely spaced tufts of desert grasses and low shrubs.

The accompanying map has been compiled chiefly as the result of information collected in the course of work which has demanded attention to various parts of the country. No systematic survey has yet been possible, although preliminary surveys of certain parts of the country, such as the Masai Reserve, the Kikuyu grass areas and parts of the Northern Frontier Province, have been made. Further, every opportunity has been taken, over a period of eight years, to gain knowledge of the extent of the vegetational types in the areas which have been visited. This map is intended as a basis for further survey, which it is hoped may be undertaken in the near future.

In the descriptions of vegetation, which accompany the map, little attention has been paid to common names of plants. The reason for this is that these names are unreliable and often misleading. Comparatively few species possess well-known common names, although there are native names for practically all. These native names are, however, derived from a number of different tribal languages which are little known to Europeans, and it is, therefore, seldom possible to give a name which is of any significance outside the area occupied by the tribe to which it belongs.

I. FOREST TYPES

(*a*) *Mountain forest.*

The most important forest areas of Kenya are situated between 6500 and 9000 ft. altitude. This is the region of typical mountain forest, but even within this zone there is considerable variation, resulting from the varying aspect of the slopes in relation to the rain-bearing winds and from the differing temperature conditions produced by altitude. The type occupies the higher land masses within the highland region of the country and occurs under a rainfall of approximately 35–90 in. per annum. In general, a belt of bamboo (*Arundinaria alpina*) is found at the upper and moister fringe of this forest, extending between 8000 and 10,000 ft. altitude, while at the lower and drier edge the forest consists mainly of cedar (*Juniperus procera*) and olive (*Olea chrysophylla* and *O. Hochstetteri*).

This mountain forest, which is essentially evergreen, appears to fall into two main types related to moisture conditions. These are (*a*) a high moisture type occurring under an annual rainfall of from 55 to 90 in. and (*b*) a lower moisture type under a rainfall of from 35 to 55 in. The former, which is confined mainly to the eastern slopes of the mountain masses, is characterized by the absence of cedar and is largely dominated by *Ocotea usambarensis* (East African camphor) and *Podocarpus milanjianus*. The latter is composed chiefly of *Juniperus procera* (cedar), *Podocarpus milanjianus* (at the higher altitudes), *P. gracilior* (at lower altitudes), *Olea Hochstetteri* (white olive) and *O. chrysophylla* (brown olive). In addition to these main species there are many species of hardwoods to be found in both types.

On the map no attempt has been made to differentiate either between the above two types or between these and the forest which lies at somewhat lower altitudes, although practically all the important forest areas of Kenya are, in fact, situated at comparatively high elevations. Below the main mountain forests detached areas of forest are frequently found at altitudes between 5000 and 6000 ft., under a rainfall of about 35 in. per annum. These contain a large variety of species such as *Brachylaena Hutchinsii*, *Croton megalocarpon*, *Olea* *chrysophylla*, *Strychnos Elliotti* and *Acokanthera Schimperi*, while cedar and white olive, which also occur, appear chiefly as comparatively small trees. Where the forest extends to still lower altitudes (3000–5000 ft.) under high rainfall, as to the north-east of Mount Kenya and near Lake Victoria Nyanza, it assumes a more tropical character. This forest consists of tall white-trunked trees, and a dense undergrowth is formed of ferns, mosses and vines. Along the streams banana is frequently found. Few of the species of this warmer, wetter forest are the same as those which occur in the foregoing types. Some of the most important are *Vitex keniensis*, *Premna maxima*, *Cordia Holstii*, *Linociera Welwitschii*, *Lovoa* sp., *Piptadenia Buchananii*, *Fagara* sp., *Celtis Durandii* var. *ugandensis*, *C. Soyauxii*, *C. Kraussiana*, *Funtumia latifolia*, *Maesopsis* sp. and *Mimusops cuneifolia*.

(*b*) *Thorn forest.*

This type occurs as scattered, comparatively small areas, chiefly in the waterless country of the acacia-desert grass savannah. It often forms almost impenetrable bush consisting mainly of various species of *Acacia*. The growth period is short and during the greater part of the year the trees are leafless. Characteristic types of this vegetation are *Acacia mellifera*, *A. spirocarpa*, *A. senegal*, *Balanites aegyptiaca*, *Boscia* spp. and, in parts, *Sansevieria* spp. In some localities, during the long dormant periods, only the leathery leafed *Boscia* presents a green appearance amongst the trees.

(*c*) *Mangrove forest*

This is a further forest type which is comparatively unimportant. One small area only is shown on the map. Such forests are confined to salt or brackish swamps in tidal creeks or deltas at the coast. The trees, which are 25 to 75 ft. high, stand on high-arched prop roots, which lift the main stem of the tree above high tide. The more important species in this forest are *Rhizophora mucronata*, *Ceriops candolleana*, *Bruguiera gymnorhiza*, *Avicennia officinalis*, *Sonneratia acida*, *Heritiera littoralis* and *Carapa obovata*.

II. GRASSLANDS, INCLUDING PARKLAND OR SAVANNAH GRASSLANDS

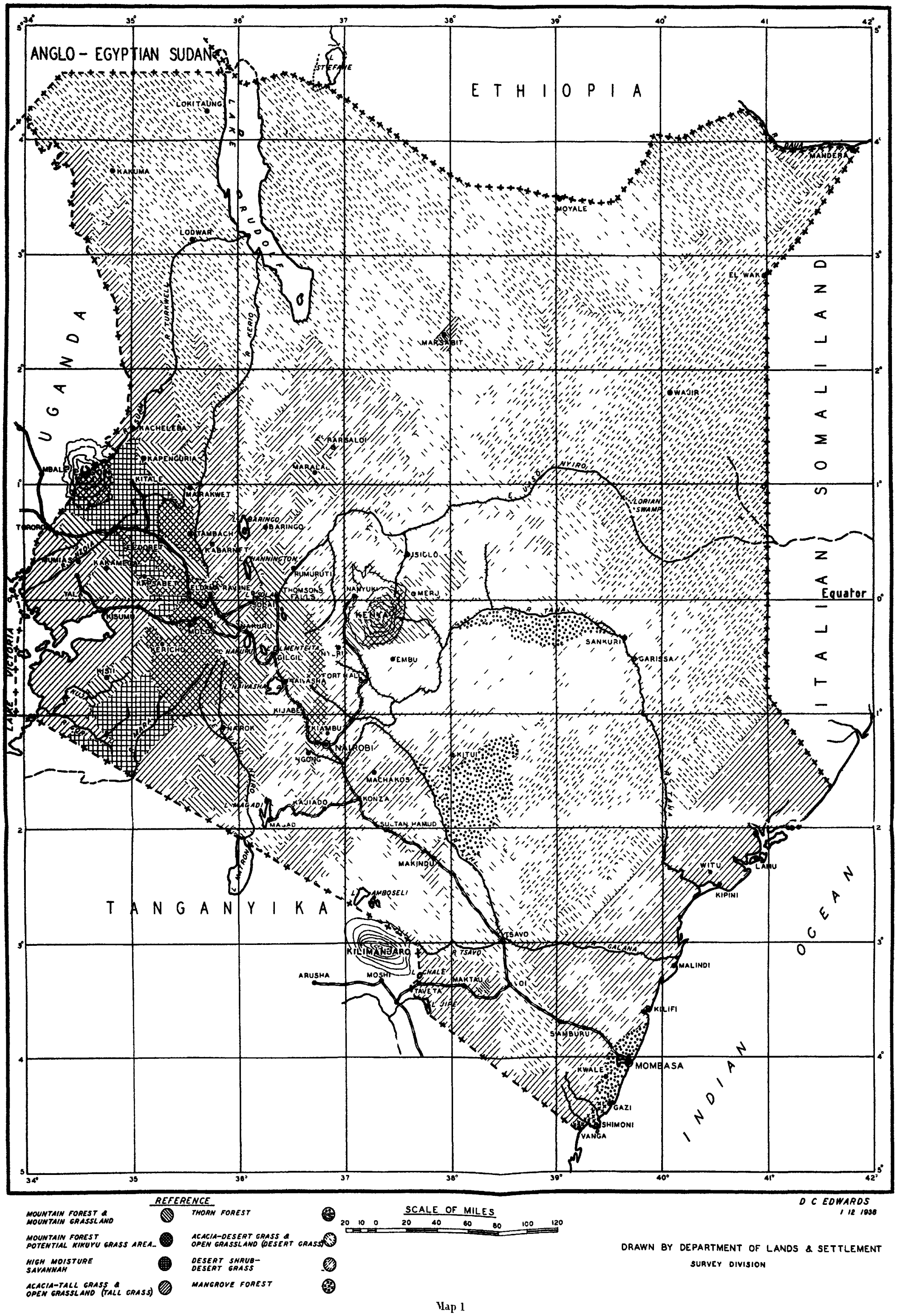
The grasslands of Kenya are by far the most important type of vegetation. If the semi-arid desert-grass areas are included in this classification, vegetation which is preponderantly grass occupies almost the whole of the country, with the exception of limited areas of forest and a considerable area to the east where more pronounced desert conditions result in a very scant cover of shrubs and grass.

(*a*) *Mountain grassland*

At approximately 10,000 ft. altitude the bamboo forest gives place to the typical mountain grassland or heathland. This is characterized at first by giant

MAP SHEWING VEGETATION OF KENYA

WITH PARTICULAR REFERENCE TO GRASSLAND TYPES



Map 1

Face page 380

heaths (*Erica* and *Philippia* spp.) and giant St John's wort (*Hypericum lanceolatum* and *H. Schimperi*) and, at the higher altitudes, by giant lobelias and groundsels. The herbage of these rolling grasslands is composed largely of *Themeda triandra*, the coarse-tufted grasses *Pennisetum Schimperi* and *Eleusine Jaegeri* and less conspicuous species, such as *Andropogon chrysostachyus*, *Agrostis* spp., *Festuca abyssinica*, *Avenastrum elongatum* and *Bromus* spp., together with *Hyparrhenia Ruprechtii* and species of *Cymbopogon*. *Pennisetum clandestinum* (Kikuyu grass) occurs chiefly as small colonies, particularly where the soil fertility is relatively high, as on the sites of old native cattle herding places.

Within the forest zone, between 6500 and 9000 ft. altitude, are considerable areas of open grassland which were, in the past, occupied by forest, and where fire, operating over long periods, has probably been the chief factor in causing the forest to recede. These areas are dominated in the main by *Themeda triandra*, but there are large and increasing areas where the tufted *Pennisetum Schimperi* is strongly dominant, and smaller areas where *Eleusine Jaegeri* occupies the land. *Pennisetum clandestinum* (Kikuyu grass) is dominant over limited areas only, where forest has been cleared within recent years. As the high soil fertility produced under forest declines where the return of the forest cover is prevented, a definite coarse-grass phase dominated by *Eleusine Jaegeri* and *Pennisetum Schimperi* appears, and later, with still further fall of soil fertility, *Themeda triandra* becomes the dominant. The greater part of this grassland type is at present in the *Themeda* stage, but this grass, under the climatic conditions of the type, is extremely sensitive to increase of fertility, such as may be caused by concentration of animals in grazing, and rapidly gives way to the coarse-grass stage. This has resulted in considerable tracts of land under European settlement changing to their present unsatisfactory condition of herbage dominated by the above-mentioned coarse species. By means of a sufficient increase in soil fertility, particularly with regard to organic matter, highly productive Kikuyu grass pastures can be produced in limited areas throughout this vegetational type. The whole of this climatic zone may, therefore, be regarded as potentially a region of Kikuyu grass pastures, where close stoloniferous swards of the grass can be maintained under intensive management. The lower limit of rainfall for the type is approximately 40 in., comparatively well distributed throughout the year, and supplemented by mountain mists. These scattered areas are shown separately on the map, where they are differentiated from the remainder of the mountain forest type.

The most characteristic species of this grassland are Kikuyu grass itself and the two large grasses, *Pennisetum Schimperi* and *Eleusine Jaegeri*. These last two appear to be strictly confined to areas above 6500 ft. altitude, although they frequently occur under moisture conditions which are too low for the success of Kikuyu grass. In addition to these species, *Themeda triandra* is the most frequent dominant, as already described, and *Hyparrhenia Ruprechtii*, *Andropogon chrysostachyus*, *A. pratensis*, *Cymbopogon* spp. and *Agrostis* spp. are all occasionally important in the herbage. Legumes are more plentiful in this vegetation than in any of the other grassland types. *Trifolium Johnstonii* is the most widely distributed and important pasture legume. It is found throughout the mountain grassland in short herbage and on arable land, but it is most characteristic of the typical Kikuyu grass areas. Other clovers which occur at the higher altitudes are *Trifolium repens*, *T. semipilosum* and *T. usambarense*.

The comparatively limited forest areas of this last described type are probably capable of higher production than any other vegetational areas of the country and, indeed, they would be difficult to equal in the world for pastoral purposes if suitable methods of management could be applied.

In addition to the two above-described mountain grassland types, there are important areas which are transitional between the Kikuyu grass vegetation and the surrounding acacia-tall grass savannah. In these areas *Themeda triandra* is the chief dominant of the herbage and Kikuyu grass is of a temporary nature and occurs in small colonies. *Pennisetum Schimperi* tends to replace the *Themeda* under grazing conditions and such coarse species as *Pennisetum catabasis* and *Sporobolus filipes* are important in localized areas.

(*b*) *High moisture savannah*

This title covers at least two distinctly different types of vegetation, and there is considerable variation within these types, but the whole is a savannah formation occurring under higher rainfall than the acacia-tall grass savannah to be described later.

Mainly towards the west of the country, where the climate is influenced by the rain-bearing winds from Lake Victoria, this vegetation is found at altitudes of from 5000 to 6000 ft. The greatest area of the type is the Trans Nzoia, to the east of Mount Elgon, where the annual rainfall is from 45 to 50 in.

In this savannah vegetation the thickly scattered trees vary from about 10–15 ft. high, and the herbage is composed of tall grasses 5–8 ft. high. Amongst the trees, species of *Acacia* are frequently important, but, typically, broad-leafed trees are more prominent. Characteristic types are *Combretum*, *Terminalia*, *Ficus* and *Faurea*. The herbage is dominated by *Themeda triandra*, *Hyparrhenia* spp. and *Cymbopogon* spp. and with these are associated a large number of other grasses such as *Chloris gayana*, *Setaria trinervia*, *Trichopteryx kagerensis*, *Digitaria diagonalis*, *Beckeropsis uniseta*, *Paspalum scrobiculatum*, and *Cynodon* spp. *Pennisetum clandestinum* occurs as small colonies throughout the higher portions of the area. Particularly towards the drier margin of the type, *Bothriochloa insculpta* and *Heteropogon contortus* become important.

To the south of this western belt of vegetation is a considerable area which does not correspond closely with the foregoing description. It is a parkland consisting of distinct groups of trees 20–50 ft. high, and a herbage in which coarsely tufted grasses are often important. The main portion of this vegetation is situated in the Trans Mara and Sotik areas. Some of the characteristic species in these tree groups are *Olea chrysophylla*, *Rhus glaucescens*, *Teclea nobilis*, *Pittosporum abyssinicum*, *Hippocratea* sp., *Acokanthera Schimperi* and *Carissa edulis*. The herbage is most frequently dominated by *Themeda triandra* and the coarse species, *Pennisetum catabasis*, is important in many parts of the area. *Pennisetum clandestinum* again occurs as small colonies in the higher portions. The annual rainfall is, in general, in the region of 50 in. or a little above.

(c) *Acacia-tall grass savannah and open grassland* (*tall grass*)

The most extensive vegetational type of the highlands of East Africa is acacia-tall grass savannah. It occurs as a belt more or less encircling the highland area and occupies all the drier parts within the highlands. It reappears as a fairly broad strip towards the coast, on the other side of the intervening arid zone. The rainfall of this type, which is 20–30 in., is erratic and droughts are a feature of the climate.

The vegetation consists typically of an even cover of grass 3–4 ft. high with widely scattered trees 10–50 ft. in height. The trees may vary considerably from one area to another, and in some parts may be only a few feet in height. There are also extensive areas practically devoid of trees.

The most frequently occurring trees are species of *Acacia*, the characteristic flat-topped trees of this type of country, although many other species may occur. Further, not all the acacias are of this appearance, as a number of species, such as the common *A. drepanolobium*, are shrubs or small trees. The most characteristic *Acacia* species are: *A. stenocarpa*, *A. abyssinica*, *A. hebecladoides*, *A. drepanolobium*, *A. lahai*, *A. pennata*, *A. seyal* and *A. xanthophloea* (near water). In the coastal belt and under the more tropical conditions towards Lake Victoria, common species are: *A. senegal*, *A. zanzibarica*, *A. arabica*, *A. Benthamii*, *A. campanulata*, *A. spirocarpa* and *A. purpurascens*. Candelabra-like *Euphorbia* species are often found in particularly dry localities and are a striking feature of the landscape, and aloes together with other succulents are also common in these areas.

In the higher, and usually moister, portions of this vegetation *Acacia* species are less important, and their place is frequently taken by sclerophyllous bush in which common species are *Combretum splendens*, *Terminalia* spp., *Rhus glaucescens*, *R. villosa*, *Acokanthera Schimperi*, *Carissa edulis*, *Euclea lanceolata* and *Commiphora* spp.

The herbage of this vegetational type consists of tall grass which, in the growing season, presents the appearance of an almost complete cover, but which is, in fact, always open at the base, and there is a considerable proportion of bare ground. The vegetation as a whole is remarkably uniform when the extensive area covered by the type is taken into consideration, and this particularly applies to the herbage, which is dominated to a very large extent by *Themeda triandra*. Other grasses which are important are *Pennisetum masaicum*, *Eragrostis* spp., *Hyparrhenia* spp., *Andropogon* spp., *Setaria* spp., *Panicum* spp. and, particularly at the drier fringe of the type, *Pennisetum stramineum* and *Digitaria* sp. aff. *D. nodosa*. Species of *Cynodon* occur chiefly in localized areas near streams and on ancient lake beds. They are frequently associated in these latter situations with extensive areas of the small tree, *Tarchonanthus camphoratus* (Ol-leleshwa, Masai). *Chloris gayana* and other *Chloris* spp. are occasional in occurrence throughout this vegetation. Legumes are, in general, comparatively scarce in the herbage and they are chiefly represented by species of *Indigofera* and *Crotalaria*.

The whole of the area occupied by this vegetation is subject to prolonged periods of drought, and during these periods fire frequently sweeps through extensive portions. Grass burning is, in fact, a deeply rooted custom of the pastoral tribes which occupy a large part of the area, and fire probably exerts a marked influence on the relative importance of the herbage species.

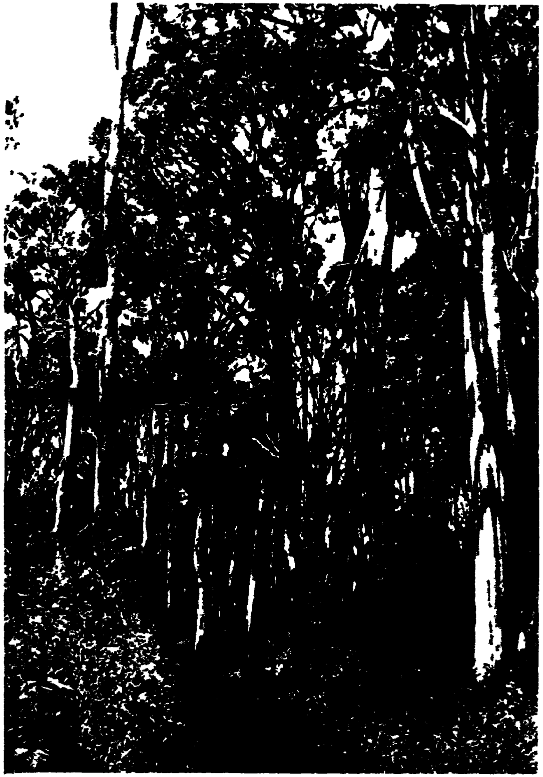
III. SEMI-ARID GRASSLANDS

(*a*) *Acacia-desert grass savannah and open grassland* (*desert grass*)

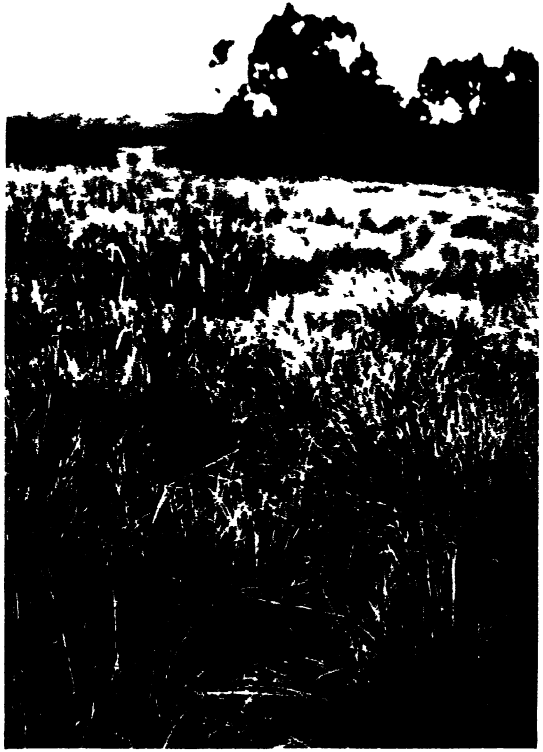
This is a very extensive type lying to the north and east of the country, mainly between altitudes of 2000 and 4000 ft. It probably occupies not less than one-third of the total land area, and together with the drier desert shrub-desert grass vegetation constitutes at least two-thirds of the total. The rainfall is from 10 to 15 in. per annum, but it is not uncommon for portions of the area to be virtually without rain for several years in succession and, apart from the short growing periods, the trees are usually in a dormant condition and the grasses dry and brittle.

The vegetation consists mainly of scattered tufts of desert grasses with widely spaced thorny trees or bushes. The reddish colour of the exposed sandy soil enters into the general tone of the landscape. Extensive areas are devoid of trees and support only isolated tufts of grass with occasional low bushes and shrubs (Phot. 4). The most common trees and bushes are *Acacia* spp., of which *A. mellifera* is often a prominent type. Species of *Commiphora* are also frequently encountered. Some of the common shrubs are *Disperma eremophilum*, *Barleria acanthoides*, *Sericocomopsis pallida*, *S. Hildebrandtii* and *Seddera latifolia*. The Doum Palm, *Hyphaene thebaica*, is characteristic of the margins of the dry stream beds.

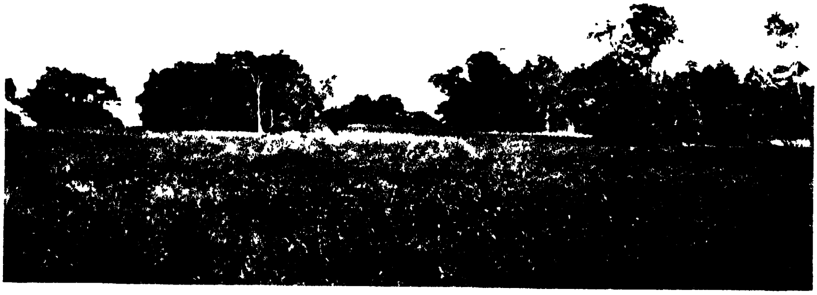
This vegetation is very imperfectly known in Kenya, but as far as it has been investigated, the most frequent dominant of the sparse grass-herbage appears to be *Chrysopogon Aucheri* var. *quinqueplumis*. *Aristida* spp. and *Sporobolus* spp. are important, and other common grasses are *Bothriochloa radicans*, *Tetrapogon spathaceus*, *T. tennellus*, and *Enneapogon* spp. Near the



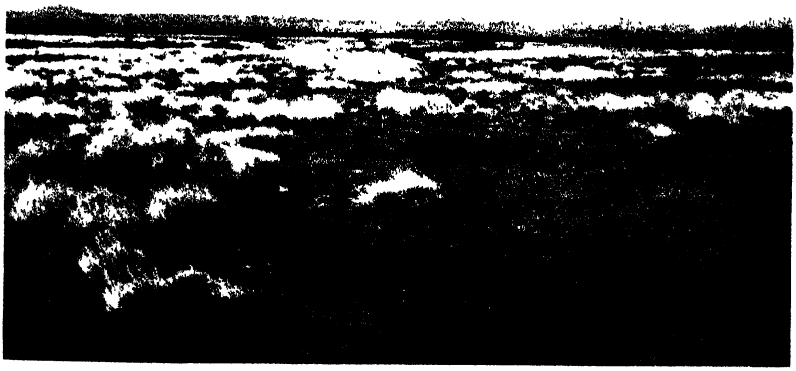
Phot. 1. Montane forest of cedar and olive. Mau Escarpment. September 1936.



Phot. 2. Montane grassland dominated by coarse *Pennisetum Schimperi* and *Eleusine Jaegeri*. Molo. October 1934.



Phot. 3. High moisture savannah with distant tree groups, Trans Mara, September 1936.



Phot. 4. Open grassland of desert grass—tufts of *Chrysopogon Aucheri*, Kaisut Desert, Northern Frontier Province, December 1932.

larger streams narrow belts of *Cynodon* spp. occur, and in other limited areas of higher moisture conditions colonies of *Cenchrus ciliaris* are encountered. Near the fringe of the type, towards the acacia-tall grass savannah and in the Thorn Forest areas, *Chloris myriostachya* is a frequent dominant of the herbage and *Digitaria* sp. aff. *D. nodosa* tends to form a short-grass cover in the open country.

(*b*) *Desert shrub-desert grass*

This type is closely allied to the acacia-desert grass savannah and desert grass vegetation. It is shown on the map covering an extensive area to the east and north-east of the country, but its extent is only vaguely known, and much of the area shown could probably be classified as desert grass. In this formation the rainfall is extremely low, and ranges from 5 to 15 in. The vegetation is essentially similar to that already described for the desert grass region, except that the arid conditions result in a preponderance of desert shrubs between which are found widely separated tufts of desert grasses.

ACKNOWLEDGEMENT

It is desired to acknowledge assistance obtained from *Trees and Shrubs of Kenya Colony* by E. Battiscombe, in dealing with the forest types in this account of the vegetation.

STUDIES OF THE VEGETATION OF THE ENGLISH CHALK

VI. LATE STAGES IN SUCCESSION LEADING TO CHALK GRASSLAND

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(*With Plate* 22 *and one Figure in the Text*)

Introduction

In studying the chalk grasslands of the Hampshire-Sussex border, Tansley & Adamson (1925, no. III of these studies) examined certain areas which showed phases of development of grassland following colonization of bared areas. Two of these sites have recently been examined again by the writer, and the combined data throw additional light upon the manner and rate of succession on the chalk.

War Down spoil banks (Pl. 22, phot. 1)

A certain amount of information about the subsere leading from bare chalk talus to grassland was obtained by Tansley & Adamson in 1920 by comparing two slopes in a disused quarry with a third one which evidently began its history some years earlier. Supplementary information is now available through an examination of the same slopes after a lapse of 16 years since the original lists were compiled. The second set of records was in fact obtained in 1936 (20 August) and in 1937 (28 June), but for the sake of simplicity the date 1936 is used alone.

(1) *History*

It is well to place these 16 years in their proper perspective in the total history of the banks. As far as can be ascertained from quarrymen and foresters in the neighbourhood, the quarry as a whole was abandoned about 1895, so that slopes (1) (south aspect) and (2) (north aspect), which are adjacent to the working face and evidently derived from the most recent operations, are about 40 years old; slope (3) (south aspect) is in the outer part of the quarry on a spoil heap which evidently accumulated earlier; the quarryman estimates that its date of origin would be about 1880. The data thus show the progress of succession on slopes (1) and (2) after periods of about 25 and 40 years, and on slope (3) after about 40 and 55 years.

Until 1932 the succession was liable to the influence of rabbits, but the intensity of their action has apparently varied a good deal. When visited by

Tansley and Adamson in 1920 the banks were not noticeably affected by rabbits, nor was most of War Down itself. The testimony of three local foresters is that just before the erection of a rabbit-proof fence (round the whole of War Down including the quarry) and the removal of the rabbits by the Forestry Commission at the end of 1932, most of War Down was heavily grazed by rabbits, and in the disused quarry there was a warren. Nevertheless it is probable that even at the time of their maximum abundance the rabbits would not graze the rather sparse vegetation of the quarry with as much vigour as the turf outside it. In short, until 1932 the banks have been under the influence of rabbits, but this has been moderate and subject to fluctuations, e.g. an increase between 1920 and 1932; and from 1932 to 1936 there has been no grazing.

(2) *Causes of change*

It is of course impossible to assume that all the differences shown by comparing the lists of 1920 and 1936 represent seral changes. A comparison, of which details will be given in a later paper, of certain chalk grasslands before and after a 15-year interval, shows that in mature grassland long-period non-successional changes of considerable magnitude occur, in addition to year-to-year fluctuations. At least three types of change are occurring on the War Down banks:

(i) These non-successional changes or fluctuations. An ascertained cause of one example of these was a landslide on slope (3) resulting in a considerable local growth of *Arrhenatherum*, *Ranunculus repens*, etc.

(ii) Changes after removal of rabbits in 1932.

(iii) The main autogenic succession.

(3) *Floristics*

Perhaps the most striking feature in the records (Table 1, Appendix, p. 398) is the increase in the number of the species on each of the three slopes.

	No. of species		
Years	Slope (1)	Slope (2)	Slope (3)
0	0	0	0
25	26	23	—
40	50	48	33
55	—	—	63

It seems that the number of species present after 25 years is approximately doubled after a further 15 years. Such quantitative conclusions cannot, however, be accepted as certain because it is possible that the 1936 survey, having been done in a fairly leisurely way, represents a more thorough search of the slopes than that of 1920, which was not done with a view to a second survey ever being undertaken. But there can be no doubt that many new species have appeared.

(4) *Specific changes*

On the right-hand side of Table 1 the species are marked into categories according to their behaviour between 1920 and 1936. The conclusions are not based on the findings of the tests of method described earlier (Hope-Simpson, 1940), because these areas are much smaller and more exactly bounded than that where the most nearly corresponding test was made. For this reason less allowance has been made for error in the present case. The species marked "vanished" (V) and "new appearance" (N) were observed only on one occasion (1920 or 1936). Since the area of each slope is small enough to study carefully, it is probable that few of even the rare species were missed on either occasion, although as already explained there is greater doubt in the case of the 1920 lists. Species are marked "significant decrease" (D) and "significant increase" (I) according to the writer's judgment of the significance of difference between symbols. In nearly all cases the practice has been followed of regarding as significant any difference greater than one unit; for example, a species recorded as o. or lf. (1920) and a. (1936) is classed under "significant increase" and marked I, but a case of f. (1920) and a. (1936) is considered as roughly stable and the space in the summarizing column is left blank.

The bulk of the species on each of the three slopes falls under either "roughly stable" or "new appearance". This would best conform with the conclusion that the main process in succession on the spoil banks at this stage is the filling in of bare spaces, partly by new species, rather than an alteration in the balance between species already present. In this connexion it should however be remembered that the field methods used are likely to detect the new arrivals, but they are not capable of detecting any but large changes in abundance. That the bare spaces have been partly filled in the interval is suggested by comparing the 1920 and 1936 estimates of the amount of bare surface, although these estimates were subjective and not arrived at by actual measurement:

Slope (1) 1920—"about 60% of bare chalk 'soil'"; 1936—25–30% of the surface bare.

Slope (2) 1920—"about 40% of the surface bare"; 1936—25–30% of the surface bare.

Slope (3) 1920—"about 10% of bare surface"; 1936—surface almost entirely covered.

On slope (1) *Festuca* was the leading colonist in 1920 with *Carex flacca* next; in 1936 no such definite statement could be made, particularly with regard to *C. flacca*, although it was everywhere quite abundant. On slope (2) the 1920 description still applied in 1936; while on slope (3) *Festuca* and *Carex flacca* were co-dominant in 1920, and in 1936 were recorded as a. and v.a. respectively.

An initial prominence of *Festuca* (mostly *ovina*) and *Carex flacca* followed by a decrease, relative to the total cover, is thus shown by both the south-facing slopes. Apart from this there appears to be no very marked difference between the course of the succession on the south-facing slope (1) and the equal-aged north-facing slope (2). The grassland now being developed on the two does however show some of the typical differences between these two aspects.

On the assumption that their behaviour is related mainly to successional change rather than to non-successional fluctuation, the species which behave in a fairly consistent manner on all three slopes are classified below to give an idea of the part played by them in the sere:

(*a*) *Anthoxanthum odoratum* is the only species which on balance has decreased. The decrease is curious, since casual observation does not suggest that the species is a pioneer on the chalk, and it is not uncommon in fully matured chalk grassland.

(*b*) Species roughly stable on at least two of the three slopes, i.e. either established early in the sere and now stable, or changing very slowly (*Echium* and *Tussilago* will doubtless disappear ultimately):

Agrostis stolonifera[1]
Avena pratensis
Carlina vulgaris
Cirsium acaule
Dactylis glomerata
Echium vulgare
Festuca ovina + rubra[2]
Hieracium pilosella
Linum catharticum

Lotus corniculatus
Senecio jacobaea
Taraxacum spp.
Thymus serpyllum
Tussilago farfara

Camptothecium lutescens
Hypnum chrysophyllum
H. cuspidatum
H. molluscum

(*c*) Species showing significant increase or new appearance on at least two of the three slopes, and at any rate no decrease if present on the third, i.e. arriving, or only finding conditions suitable, later in the sere:

Arrhenatherum elatius[3]
Brachypodium sylvaticum
Briza media
Deschampsia caespitosa
Gentiana axillaris
Heracleum sphondylium[3]
Holcus lanatus
Koeleria cristata
Leontodon hispidus
Orchis maculata[3]
Plantago lanceolata
Poa pratensis
Prunella vulgaris

Solanum dulcamara
Sonchus oleraceus
Trifolium pratense
T. repens
Trisetum flavescens
Veronica chamaedrys

Crataegus monogyna[3]

Brachythecium purum
Bryum capillare
B. inclinatum
Ditrichum flexicaule

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[1] For angiosperms the nomenclature in this paper follows a list prepared by Dr T. A. Sprague for *The British Islands and their Vegetation* (Tansley, 1939). Messrs N. Y. Sandwith and V. S. Summerhayes have kindly corrected certain names which were not in this list. The name *Carex diversicolor* used in Tansley's book has been replaced by *C. flacca*, following the findings of Nelmes & Sprague (1939). *Festuca ovina* and *F. rubra* are considered jointly on account of the difficulty in assessing their frequencies separately. The bryophyte names are those of Dixon (1924). Capitals have been deliberately omitted for all specific names.

[2] But see bottom of previous page.

[3] New appearance probably related to removal of rabbits rather than, or in addition, to succession.

The spread of *Arrhenatherum* has probably been aided by all three of the agencies mentioned on p. 387 (landslide, removal of rabbits, and succession).

(5) *Discussion*

It is clear that the succession is a relatively slow process, but it is equally clear that some visible change has been made during the 16 years' interval towards a more fully developed grassland.

The progress in floristic composition which has evidently occurred is no doubt due to three contributory causes:

(1) Maturation of the habitat (soil formation, etc.).

(2) Spreading of species already present, giving a higher frequency.

(3) Later arrival of the propagules of rarer species or of species with slow dispersal.

The sere is not yet complete and a fourth factor will be loss of species by competition, but this does not seem to have occurred perceptibly during the period 1920–36. It is not surprising if the competitive phase does not come until the end of the sere when the bare spaces are mostly filled. A number of species which as yet show no decrease would without doubt disappear ultimately (e.g. *Echium* and *Tussilago*; and *Arrhenatherum* if the banks were open to grazing). These and various other species on the slopes are not constituents of mature chalk grassland.

The incompleteness of the sere is shown not only in the presence of species which will finally disappear. At least two common species are absent which, but for the imminent creation of a forest on War Down, could reasonably be expected to establish themselves on the spoil banks in time; these are *Scabiosa columbaria* and *Hylocomium squarrosum*, which are both abundant in the vicinity and almost certainly capable of accommodating themselves to the physiographic conditions of at least one of the slopes. *Poterium sanguisorba* is an important chalk grassland plant which was absent from all the slopes in 1920 and is now rare on slope (3). It happens to be unusually rare on War Down and the adjoining Butser Hill, and in any other chalk grassland region might have appeared a good deal sooner in the succession than it has on these spoil banks.

It is worth noting that the vegetation of the banks, which, except for the last four years, has been subject to grazing, is to be regarded as a stage leading to grassland under the biotic influence responsible for the maintenance of grassland, and not as a stage in the sere leading directly from exposed chalk to climax forest. That grazing has had a real influence on the course of events on the spoil banks is suggested by the fact that the period 1895 (1880 for slope (3)) to 1920 resulted in two records of woody plants, while by 1936 there were eight records, although the banks are a fair distance (about 100 yards, = 90 m.) from any big concentration of scrub. Considering that rabbits have been completely excluded for only four years (1932–6), this prompt invasion, compared with the slow development of the herbaceous vegetation since 1920, makes it likely that, in the absence of grazing, woody invaders would dominate the area before the herbaceous vegetation could become mature. In actual fact the afforestation of War Down may prevent a natural sequence on the banks from deciding between these alternatives.

This picture of the seral changes of course applies to a habitat under particular conditions. The substratum of "spoil" is broken and easily penetrable by roots, and all three slopes are steep: Slope (1) 28–42°, average *c.* 35°; (2) 28–38°, average *c.* 35°; (3) 30–38°. There are no data of a comparable kind showing the succession from bare chalk on a flat or gently sloping site. The only case of succession studied on more or less level ground is provided by the colonization of the old arable area at Coulter's Dean which will now be described.

COULTER'S DEAN "WASTELAND" (Pl. 22, phot. 2)

This area, last ploughed some time before 1889, was first listed by Tansley & Adamson in 1914. In 1920, when they listed it again, it was "little if at all pastured" (Studies, III). It is now divided into two parts of very unequal size by a wire fence erected across the narrow end about 1929, perhaps earlier. The main area, A, south of this fence, covering about 4 acres (1·6 hectares), has for several years been grazed by rabbits and sheep, while the small area B, of about ⅓ acre (0·13 hectare) is not grazed and bears tall herbage largely composed of *Arrhenatherum* and containing many woody plants, although these are still isolated. A and B were listed separately in 1936 (8 and 25 September). The data are given in Table 2 (Appendix, p. 400).

(1) *Floristics*

The numbers of species found in 1920 and 1936 cannot be taken with any certainty as significant data on account of the personal factor in recording (Hope-Simpson, 1940, p. 206), but the total flora of the area seems to be about the same in number in 1936 as it was in 1920 (within the probable limits of error).

The numbers of species, including woody plants, held in common by the list of 1920 and those of 1936 A and 1936 B respectively, expressed as percentage of the number of species in the shorter list, are: 1920 and 1936 A, 77%; 1920 and 1936 B, 68%. The figures suggest that since 1920 area B (ungrazed) has changed more than A in floristic content.

A curious detail of the records is the absence from them all of *Koeleria cristata*, whose constancy in chalk grassland is the maximum value, 5.

(2) *Specific changes*

Examining the records of species individually, there is only one case which, in view of the errors (Hope-Simpson, 1940), permits a definite statement to be made as to change in abundance. This is in the fine-leaved fescues, which have become more prominent on area A (l.→f.–v.a.).

Much information, however, as to the type and quantity of change can be gathered by considering species in categories.

(3) *Woody plants*

A careful search was made for these in 1936. Results, as numbers of species found, are as follows:

1914	1920	1936 *A* + *B*	1936 *A*	1936 *B*
14	19	14	9	12

It is quite clear that the onset of grazing on area A has reduced the number of woody species. The possibility that the deficiency is explained by the fencing off of some of the woody plants in the small area B is disposed of by the fact that the total for A + B in 1936 is well below that of 1920. It seems safe enough to say that the following eight early woody colonists have been grazed out since 1920:

Betula pendula
Clematis vitalba
Pyrus malus
Quercus robur
Rosa arvensis
R. rubiginosa
Sorbus aria
Viburnum lantana

(4) *New arrivals*

The species of flowering plants found in 1936 but not in 1914 or 1920 are given below. The figures for the constancy of the species in mature chalk grassland are in the main the same as those given by Tansley & Adamson (1926; Studies, IV):

On both A (grazed) and B (ungrazed)

	Constancy
Cerastium vulgatum	3
Cirsium lanceolatum	2
Crepis capillaris	1
Galium cruciata	1
Ranunculus repens	1
Taraxacum officinale	1
Urtica dioica	0
Mean constancy	1·3

On A (grazed) only

	Constancy
Galium verum	4
Hypochaeris radicata	1
Leontodon nudicaulis	1
Stachys sylvatica	0
Mean constancy	1·5

On B (ungrazed) only

	Constancy
Achillea millefolium	4
Bartsia odontites	1
Caucalis anthriscus	1
Geranium dissectum	0
Lathyrus pratensis	1
Lolium perenne	1
Poa pratensis	2
Sonchus asper	1
Vicia sepium	0
Viola sp. (? riviniana)	1
Euonymus europaeus	0
Mean constancy	1·1

It is noteworthy that a considerably larger number of new arrivals has appeared on the ungrazed part, in spite of its much smaller area. The mean constancy of the new arrivals is low, most of the chalk grassland constants having arrived much earlier.

(5) *Species of high and low constancy*

In Fig. 1 the average frequency of certain groups of flowering plants is plotted for 1914 and 1920, and separately for the grazed and ungrazed parts in 1936. The groups of species plotted are those having constancies in mature chalk grassland of 5 (almost ubiquitous in the community), 3 (of intermediate constancy), 1 (rare) and 0 (absent from mature chalk grassland). The groups of constancy 4 and 2 are omitted in order to simplify the figure. Their results conform with those shown.

Although in assigning frequencies in the field, allowance is automatically made for the different sizes of the two areas, such allowance cannot be made for a species which is altogether absent from the smaller area. It is likely that a number of species represented in A are missing from B solely on account of its small size. If the areas were the same size, the divergence between the two 1936 points for the two upper curves (constancy 5 and 3) would probably be less; and for the two lower curves (constancy 1 and 0) greater. The essential conclusion would be the same.

Although the points represent the means of frequencies of not less than fourteen species, their exact position is doubtful owing to the unavoidable errors in recording the species and their frequency by the subjective method. Likely limits of error arising from this cause are shown in Fig. 1 by the line drawn across the curve for constancy 3. This estimate of error, in default of a more exact one, has been obtained by calculating the mean frequencies of fifteen species of constancy 3 (the group on the whole liable to greatest error), in duplicate lists made on the same area of grassland for a test of "inevitable error" (Hope-Simpson, 1940, p. 194). The mean frequency values for the duplicate lists were, in units of the arbitrary scale in the figure, 37 and 41, and the divergence of 4 units must be allowed for above and below the actual value obtained.

The difference in mean frequency for the grazed and ungrazed parts of the Coulter's Dean area is most marked in the case of the species of constancy 5. If the evidence of Fig. 1 be accepted, these and the group of constancy 3 have increased in abundance on the grazed part of the area, while in the absence of grazing they maintain themselves as colonists in the early phases (1914 and 1920) but when the community grows dense (1936 B) they show a pronounced decline. Species of constancy 1, i.e. those found in mature chalk grassland, but not at all regularly, and of constancy 0, i.e. species not found in mature chalk grassland, become more abundant in the absence of grazing and suppressed in its presence.

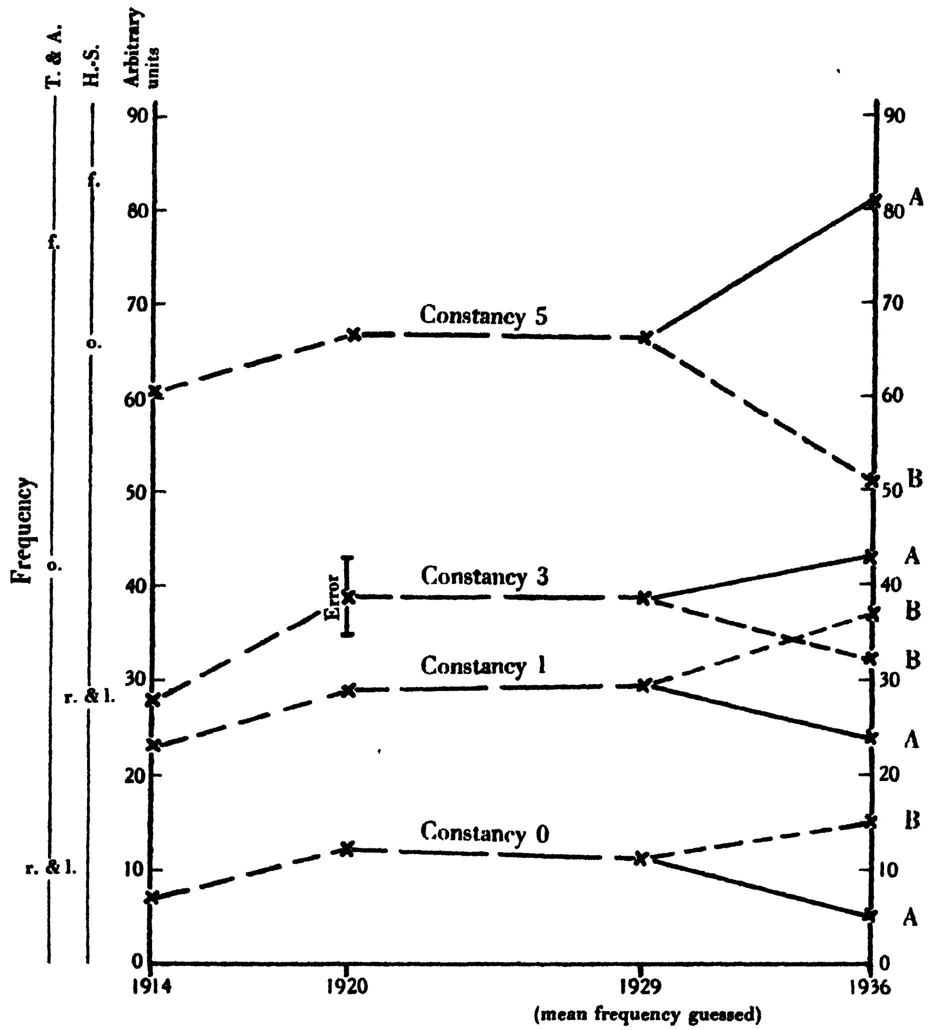

Fig. 1. Mean frequency in Coulter's Dean grassland of herbaceous flowering plants grouped according to their constancy in chalk grassland. Constancy 5, 14 spp.; constancy *c.* 3, 15 spp.; constancy 1, 35 spp.; constancy 0, 21 spp. Frequencies were recorded in 1914 and 1920 by Tansley and Adamson and in 1936 by the writer. 1929 was the approximate year of the separation by a fence of area A, grazed, from B, ungrazed, but moderate grazing on the whole area may have begun earlier. The estimate of frequency for 1929 is therefore obtained by interpolation between the value for 1920 and the mean of the two for 1936. The two scales of subjective frequency are those of Tansley and Adamson and of the writer respectively.

— — — — Ungrazed.
——— ——— Slightly grazed.
———— Well grazed.
I Range of error of mean frequency values (see text).

(6) *Discussion*

Of the Coulter's Dean area, Tansley & Adamson wrote (1925) "Pastured it would doubtless become chalk grassland with fair rapidity". The prediction is now almost fulfilled by area A. Although not exactly typical chalk grassland, it now has the essential constituents and structure of the grazed grasslands of wooded regions, the constant species, shown by Tansley & Adamson (1926) to have a high average frequency in chalk grassland in general, being present in abundance. But this progress only takes place under the influence of grazing.[1] In its absence the subsere beginning with colonization of arable land leads to a herbaceous community lacking a strong representation of the constants and containing instead many species of low constancy in chalk grassland. Area B bears a number of species which are almost or quite alien to chalk grassland even when unpastured, enabled to colonize on the exclusion of grazing because the community was immature. The grassland produced, in fact, is not chalk grassland as generally known. Preponderance of *Arrhenatherum* is not a common feature of mature chalk grassland, even unpastured, the expanses of it which sometimes occur being almost always associated with evidence of local soil disturbance. It appears likely that this is also true of chalk grassland in the Paris basin. Allorge (1922) studied nineteen *Arrhenatherum* communities, evidently stable, in the "Vexin français" (Seine-et-Oise). Of these only three were grazed, and none was on the chalk, where he studied twelve other grasslands. In dealing with dry calcareous grassland, he mentions *Arrhenatherum* as locally dominant in areas of abandoned cultivation, talus or quarries; apparently this refers mainly to the "calcaire grossier" (Eocene).

It is possible that an ungrazed sere starting on chalk talus or abandoned arable land might lead to dominance by *Bromus erectus* or *Brachypodium pinnatum* in regions where either of them is common (they are rare on the chalk of the Hampshire-Sussex border), producing a community much like that resulting from invasion of mature chalk grassland by these grasses on removal of grazing. Allorge (1922, p. 175) names both species as rapidly colonizing bared areas, but adds that the secondary grassland on such sites differs from the ancient swards, particularly in the absence of the "exclusive" and most of the "elective" species. He does not, however, mention the status of grazing in these cases.

The attainment of a stable type of subclimax grassland on area B will probably be overtaken by an invasion of shrubs. Even by 1936 the small area of B had twelve woody species, against the nine of the large expanse of A. "Left to itself it would revert to woodland" (Tansley & Adamson, 1925).

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[1] A parallel case has been observed on the North Downs near East Clandon, Surrey. A shallow valley, where ploughing was abandoned about fifty or sixty years ago, now bears juniper-dotted chalk grassland which is quite typical save for (1) abnormal abundance of *Brachypodium sylvaticum*, *Clinopodium vulgare*, *Origanum vulgare* and similar chalk "wood-edge" and "bared ground" species, and (2) the soil, which like that of Coulter's Dean has an obliterated profile and the pale grey-brown colour characteristic of arable chalk soils. The succession has taken place under rabbit-grazing.

GENERAL CONCLUSIONS

The information provided by these two areas as to the later course of the succession leading to the establishment of chalk grassland, although fragmentary, clarifies the status of the community beyond doubt. The development of "chalk grassland" as usually understood, under the influence of grazing but not without it, is a clear case of deflected succession (Godwin, 1929) or plagiosere (Tansley, 1935), and the stable grassland resulting is best called plagioclimax. The term "subclimax", although it may embrace "plagioclimax", is not unambiguous and is in this case better avoided, because typical chalk grassland does not appear to any extent as a stage in the ungrazed subsere between a bared area and the climax woodland. There is plentiful evidence, not only from the War Down banks and Coulter's Dean, but from quarries and bared areas generally, that an advanced herbaceous vegetation is not a necessary precursor to woody colonization on broken chalk, arable land or clear-felled woodland; if woody plants occur in the immediate vicinity they enter while the herbaceous colonization is at an early stage (cf. Adamson, 1922, pp. 165, 166)—at exactly what stage doubtless depends largely on the distance away of seed parents of woody plants. In the absence of woody colonists and of grazing the herbaceous community produced on a penetrable chalky surface would not, according to the evidence in the present paper, develop into chalk grassland of any ordinary kind, except perhaps in very dry or exposed situations. What it would become is doubtful. *Arrhenatherum elatius*, which shows an increase on the spoil banks as well as at Coulter's Dean, seems a possible stable dominant, at any rate in a region where *Bromus erectus* and *Brachypodium pinnatum* are both absent, as in the present case. In this connexion it is interesting that on many roadsides in chalk country, where the soil has probably at some time been disturbed and where scrub is kept away by annual cutting instead of by grazing, *Arrhenatherum* is in fact the general dominant.

The subseres on chalk talus or arable soil are relatively short because the substrate is broken and in one case contains humus. A solid chalk surface would provide very different conditions. Observations on the colonization of such a habitat were made by Tansley & Adamson (1925, pp. 180, 182–3). The colonists consisted of a numerous assortment of species, largely decided by the neighbouring vegetation. "The mixed 'community' clearly does not stand in a normal line of succession." In any case the course of succession on solid chalk would only be of academic interest, since the original development (prisere) of chalk vegetation when the chalk first became uncovered cannot have proceeded under conditions anything like those of to-day, and at the present time bare surfaces of chalk rock arise solely through human action (except on the sea-coast) and are very limited.

Phot. 1. War Down spoil banks, from the west (19. iv. 40). Slopes (1) and (2) form the right and left sides respectively of the uppermost bank, immediately against the quarry face. Slope (3) forms the right side of the central "tongue" in the left centre of the picture.

Phot. 2. Coulter's Dean "wasteland" (4. vi. 40). In the foreground, up to the fence, is the ungrazed area B. *Arrhenatherum elatius* preponderates in the herbage, and the small shrubs are mostly *Rosa*. The grassland beyond the fence in the centre of the picture is area A, grazed by rabbits and sheep.

SUMMARY

An account is given of the late stages of succession on two areas first examined by Tansley & Adamson (Tansley & Adamson, 1925). The substrate of one is broken chalk talus or "spoil", of the other formerly ploughed chalk soil.

On the spoil banks, formed in a quarry 40-55 years ago, there has been in the last 16 years an appreciable progress towards more mature chalk grassland, particularly through the filling of bare spaces. The prominence of *Festuca ovina* and *Carex flacca* seen on the south-facing slopes in 1920 has been reduced. Consequent upon the exclusion of rabbits in the last four years there has been a divergence marked by the entry of woody plants.

The old arable area, abandoned for the last 50 years or more, of which lists made in 1914, 1920 and 1936 have been compared, was about 1929 divided into two parts, one grazed, the other not. The grazed part has shown a pronounced progress towards chalk grassland since 1920, seen particularly in the increase of the fine-leaved fescues. The ungrazed part has become covered by herbaceous growth quite unlike ungrazed chalk grassland, *Arrhenatherum elatius* being the leading species, and the constant members of chalk grassland being present in much less than their usual abundance. Woody invasion is proceeding apace.

The two areas studied make it clear that the subsere from bared and broken ground on the chalk leads to typical chalk grassland only if grazing is in force; at least this is true in a region lacking *Bromus erectus* and *Brachypodium pinnatum*. Otherwise there is scrub invasion among the early herbaceous colonists, or in the absence of scrub a herbaceous cover is produced which, except perhaps in very dry or exposed situations, is not chalk grassland in the ordinary sense. Mature chalk grassland is therefore to be regarded as a "plagioclimax" produced by a deflecting factor (grazing), and not as an arrested stage in an ungrazed succession between bare ground and woodland.

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APPENDIX

Table 1. *War Down spoil banks. Records of* 1920 *and* 1936, *and summary of changes*

(1), (2) and (3) represent the three slopes. V = vanished, D = significant decrease, I = significant increase, N = new appearance. A blank space in the summary of changes means that no conspicuous change has occurred and the species is considered to be roughly stable.

	Primary data						Summary of changes		
	(1)		(2)		(3)		(1)	(2)	(3)
	1920	1936	1920	1936	1920	1936			
Achillea millefolium	—	—	—	—	o.	r.	—	—	—
Agrostis stolonifera	f.–a.	l.f.	a.–f.	f.–a.	a.	o.–l.a.	—	—	D
Anthoxanthum odoratum	f.	—	r.	—	f.	r.	V	V	D
Arctium sp.	—	—	—	—	—	r.	—	—	N*
Arrhenatherum elatius	—	l.	o.l.	o.–l.c.d.	—	l.–l.d.	N	I	N†
Asperula cynanchica	o.	f.	—	—	o.	a.	—	—	I
Avena pratensis	o.	l.	o.	r.	o.	f.	—	—	—
A. pubescens	—	r.	—	—	—	—	N	—	—
Bellis perennis	—	r.	—	—	o.	—	N	—	V
Brachypodium sylvaticum	—	r.	—	—	—	l.	N	—	N
Briza media	—	f.	—	r.	—	f.	N	N	N
Campanula rotundifolia	—	—	—	—	o.	l.	—	—	—
Carex caryophyllea	—	—	—	—	l.	—	—	—	V
C. flacca	l.a.	a.	l.	a.	c.d.	a.	—	I	D
Carlina vulgaris	f.	o.	o.	—	o.	o.	—	V	—
Cirsium acaule	l.f.	f.	o.	r.l.	v.a.	v.a.	—	—	—
C. arvense	—	—	—	l.	—	—	—	N	—
C. palustre	o.	—	—	—	—	—	V	—	—
Crepis capillaris	—	r.	—	—	—	—	N*	—	—
Cynoglossum officinale	—	—	r.	—	—	—	—	V	—
Dactylis glomerata	o.	o.	l.	r.	l.	f.	—	—	I
Deschampsia caespitosa	—	—	—	r.	—	l.f.	—	N	N
Echium vulgare	l.f.	o.–f.	—	r.	o.–f.	o.	—	N	—
Epilobium angustifolium	—	—	—	r.	—	—	—	N	—
Eupatorium cannabinum	—	—	—	—	—	r.	—	—	N
Euphrasia nemorosa	o.	r.	—	—	—	r.	—	—	N
Festuca ovina + rubra	v.a.	v.a.	v.a.	v.a. l.c.d.	c.d.	v.a.	—	—	—
Galium erectum + mollugo	—	—	—	r.	—	—	—	N	—
Gentiana axillaris	l.a.	o.	—	l.	—	o. l.f.	—	N	N
Heracleum sphondylium	—	—	—	r.	—	r.	—	N	N
Hieracium pilosella	f.	f.	o.	l.	o.	l.	—	—	—
Holcus lanatus	—	o. l.v.a.	—	f.	—	r.	N	N	N
Hypericum perforatum	—	—	—	—	—	r.	—	—	N
Koeleria cristata	—	r.	—	—	—	l.f.	N	—	N
Leontodon autumnalis	—	—	—	o.	—	—	—	N	—
L. hispidus	o.	a.	o.	a.	f.–a.	a.	I	I	—
Linum catharticum	f.	a.	f.	f. l.a.	o.–f.	a.	—	—	I
Listera ovata	—	—	—	r.	—	—	—	N	—
Lotus corniculatus	a.	a. l.d.	f.	l.a.	f.	a.	—	—	—
Medicago lupulina	—	—	—	—	—	l.f.	—	—	N
Myosotis arvensis	—	—	r.	—	—	r.	—	V	N*
Ophrys apifera	—	r.	—	r.	l.	—	N	N	V
Orchis maculata	—	r.	—	r. l.a.	—	r.	N	N	N
Pimpinella saxifraga	—	—	—	—	—	r.	—	—	N
Plantago lanceolata	—	a.	—	r.	o.	f.	N	N	—
P. media	—	—	—	r.	—	—	—	N	—
Poa pratensis	—	r.	—	—	—	r. l.a.	N	—	N
Polygala vulgaris	—	—	—	r.	—	—	—	N	—
Poterium sanguisorba	—	—	—	—	—	r.	—	—	N
Prunella vulgaris	—	o.	—	r.	—	o.	N	N	N
Ranunculus bulbosus	—	—	—	—	f.	—	—	—	V

Table 1 (*continued*)

	Primary data						Summary of changes		
	(1)		(2)		(3)				
	1920	1936	1920	1936	1920	1936	(1)	(2)	(3)
R. repens	—	—	—	—	—	l.	—	—	N*
Senecio jacobaea	—	o.	o.	o.	o.	r.	N	—	—
Solanum dulcamara	—	r.	—	r.	—	r.	N	N	N*
Sonchus oleraceus	o.	r.	—	r.	—	r.	—	N	N
Taraxacum spp.	f.	l.	f.	o.	o.	r.	D	—	—
Thymus serpyllum	f.	a.	l.a.	l.f.	f.	a.	—	—	—
Trifolium pratense	—	r.	—	—	—	l.	N	—	N
T. repens	—	r.	—	r.	—	—	N	N	—
Trisetum flavescens	—	r.	—	o.	—	f.	N	N	N
Tussilago farfara	l.d.	o. l.v.a.	a. l.d.	a. l.v.a.	—	—	—	—	—
Veronica chamaedrys	—	r.	—	—	—	r.	N	—	N*
Woody plants									
Clematis vitalba	r.	—	—	r.	—	r.	V	N	N
Crataegus monogyna	—	r.	—	—	—	r.	N	—	N
Rosa canina	—	—	—	r.	r.	r.	—	N	—
Rubus fruticosus (agg.)	—	—	—	—	—	r.	—	—	N*
Sorbus aria	—	—	—	—	—	r.	—	—	N
Bryophytes									
Barbula rigidula	—	—	—	—	o.	—		—	V
Brachythecium purum	—	r.		l.v.a.	l.a.	l.	N	N	—
B. rutabulum	—	—	—	r.	—	—	—	N	—
Bryum capillare	—	r.	—	r.	—	—	N	N	—
B. inclinatum	—	r.	—	—	—	r.	N	—	N
Camptothecium lutescens	f.	f. l.a.	f.–a.	l.a.	v.a.	f.	—	—	D
Cylindrothecium concinnum	—	—	—	—	—	r.	—	—	N
Ditrichum flexicaule	—	r.	—	r.	—	r.	N	N	N
Fissidens taxifolius	—	r.	—	—	l.a.	r.	N	—	—
Hylocomium triquetrum	—	—	—	r.l.	—	—	—	N	—
Hypnum chrysophyllum	o.	r.	l.f.	f.	—	l.f.	—	—	N
H. cuspidatum	—	r.	o.	f.	o.	r.	N	—	—
H. molluscum	f.	a.	l.a.	f.	f.	—	—	—	V
Neckera complanata	o.	l.a.	—	—	—	—	—	N	—
N. crispa	—	—	—	r.	l.	l.a.	—	—	—
Thuidium abietinum	—	f.	—	—	a.	f.	N	—	—
Trichostomum crispulum	—	—	—	—	—	l.a.	—	—	N
Lophozia turbinata	—	—	—	—	—	r.	—	—	N
Lichen									
Collema pulposum	—	—	—	—	—	r.–l.a.	—	—	N
Total number	26	50	23	48	33	63			

* On a small landslide. † Partly on a small landslide.

Table 2. *Coulter's Dean "wasteland". Records of* 1914 (*Tansley & Adamson*), 1920 (*T. & A.*) *and* 1936

A = grazed area; B = ungrazed area.

	1914	1920	1936 A	1936 B
Achillea millefolium	—	—	—	r.
Agrimonia eupatoria	o.	l.o.	r.	o.
Agropyron repens	—	r.	—	r.
Agrostis spp.	o.	o.	o.–l.d.	f.
Anacamptis (Orchis) pyramidalis	—	o.	—	—
Anthoxanthum odoratum	—	o.	—	—
Anthyllis vulneraria	o.	o.–l.f.	r.	—
Arenaria serpyllifolia	—	r.	—	—
Arrhenatherum elatius	l.	l.a.–l.d.	—	a.–l.d.
Asperula cynanchica	o.	o.	o.	—
Avena pratensis	l.	o.	r.–l.a.	—
A. pubescens	o.	o.	r.	r.
Bartsia odontites	—	—	—	r.
Bellis perennis	r.	—	r.	—
Blackstonia perfoliata	l.o.	l.o.	r.	—
Brachypodium sylvaticum	a.	a.–l.d.	f. l.c.d.	l.
Briza media	f.	f.	l.f.	r.
Calamintha acinos	r.	o.	—	—
Campanula glomerata	o.	f.	o. l.f.	r.
C. rotundifolia	—	l.	—	—
Carex flacca	a.	a.	f.–v.a.	r.
Carlina vulgaris	o.	o.	r.	—
Caucalis anthriscus	—	—	—	o.
Centaurea nemoralis	o.	l.a.	o.	f. l.a.
C. scabiosa	o.	l.f.	r.	r.
Centaurium umbellatum	o.	o.	r.	—
Cerastium vulgatum	—	—	r.	r.
Chrysanthemum leucanthemum	o.	o.–f.	l.	r.
Cirsium acaule	o.	o.	o.	—
C. arvense	—	r.	r.	l.
C. lanceolatum	—	—	l.	r.
Clinopodium vulgare	o.	l.f.	l.	o.
Conopodium majus	r.	—	—	—
Crepis capillaris	—	—	r.	r.
Cynosurus cristatus	r.	—	—	r.
Dactylis glomerata	f.	f.	f.	a.
Daucus carota	o.	o.	r.	l.
Epipactis latifolia	l.	—	—	r.
Euphrasia nemorosa	o.	o.	l.	l.
Festuca ovina + rubra	l.a.	l.	f.–v.a.	a.
Filipendula ulmaria	—	r.	—	—
Fragaria vesca	o.	l.a.	r.	r.
Galeopsis angustifolia	—	r.	—	—
Galium cruciata	—	—	r.	l.f.
G. erectum + mollugo	o.	f.–a.	l.	l.a.
G. verum	—	—	r.	—
Gentiana axillaris	o.	l.f.	o.	—
Geranium columbinum	—	r.	—	—
G. dissectum	—	—	—	r.
Gymnadenia conopsea	r.	r.	—	—
Helianthemum nummularium	o.	l.	l.	—
Heracleum sphondylium	r.	o.	r.	f.
Hieracium pilosella	l.a.	l.a.	l.	—
Holcus lanatus	o.	o.	l.f.	o.
Hypericum hirsutum	—	o.	—	o.
H. perforatum	o.	f.	r.	o.
Hypochaeris radicata	—	—	r.	—
Knautia arvensis	f.	f.	r.	o.
Lathyrus pratensis	—	—	—	f. l.a.
Leontodon hispidus	—	v.a.	a.	f.
L. nudicaulis (Thrincia hirta)	—	—	r.	—

Table 2 (*continued*)

	1914	1920	1936 A	1936 B
Linum catharticum	f.	f.–a.	a.	r.
Lolium perenne	—	—	—	r.
Lotus corniculatus	a.	a.	a.	o. l.a.
Medicago lupulina	o.	f.	o.	o.
Ononis repens	o.	l.a.	l.	—
Ophrys apifera	o.	r.	—	r.
Orchis maculata	o.	o.	—	—
Origanum vulgare	f.	a.	f.?	f. l.a.
Pastinaca sativa	o.	l.	r.	l.
Phleum pratense	—	r.	—	l.
Pimpinella saxifraga	l.a.	o.–f.	l.	o.
Plantago lanceolata	o.	f.	f.	a.
Platanthera chlorantha	—	r.	—	—
Poa pratensis	—	—	—	o.
P. trivialis	—	r.	—	—
Polygala vulgaris	o.	o.	o.	—
Potentilla reptans	—	o.	l.f.	f.
Poterium sanguisorba	a.	a.	f.	o. l.f.
Primula veris	l.	l.	r.	o.
Prunella vulgaris	o.	f.	r.	r.
Ranunculus repens	—	—	l.f.	o. l.f.
Rumex crispus	—	r.	—	r.
Sanicula europaea	—	r.	—	—
Scabiosa columbaria	l.	l.	o.–f.	—
Senecio erucifolius	—	l.	—	o.
S. jacobaea	—	r.	r.	—
Silene cucubalus	o.	l.	—	—
Sonchus asper	—	—	—	r.
Stachys sylvatica	—	—	r.	—
Succisa pratensis	l.	l.a.	o.–f.	—
Taraxacum officinale	—	—	r.	r.
Thymus serpyllum	a.	a.–l.d.	o. l.f.	r.
Trifolium pratense	o.	l.	a.	a.
T. procumbens	o.	o.	r.	r.
T. repens	l.	o.	l.a.	f.
Trisetum flavescens	a.	o.	r.	—
Tussilago farfara	r.	r.	—	—
Urtica dioica	—	—	r.	r.
Verbascum nigrum	r.	r.	—	l.
Veronica chamaedrys	r.	—	r.	f. l.a.
Vicia cracca	o.	o.	r.	o. l.a.
V. hirsuta	r.	r.	—	—
V. sepium	—	—	—	r.
Viola hirta	l.	l.a.	o.	r.
Viola sp. (? riviniana)	—	—	—	r.
	Woody plants			
Betula pendula	—	l.	—	—
Clematis vitalba	r.	o.	—	—
Cornus sanguinea	o.	o.	r.	r.
Corylus avellana	o.	o.	l.f.	r.
Crataegus monogyna	o.	o.	r.	r.
Euonymus europaeus	—	—	—	r.
Fagus sylvatica	r.	r.–o.	l.	—
Fraxinus excelsior	r.	—	—	r.
Prunus spinosa	o.	o.–l.d.	o.–l.d.	r.
Pyrus malus	—	r.	—	—
Quercus robur	r.	r.	—	—
Rhamnus catharticus	—	r.	—	r.
Rosa arvensis	—	o.	—	—
R. canina	r.	r.	o.	f.
R. micrantha	—	r.	o.	—
R. rubiginosa	r.	r.	—	—
Rubus caesius	f.	l.a.	r.	l.f.
R. leucostachys	—	—	—	l.

Table 2 (*continued*)

	1914	1920	1936 A	1936 B
Rubus ulmifolius	—	l.	r.	r.
Salix caprea	o.l.	o.l.	—	r.
Sorbus aria	r.	o.	—	—
Viburnum lantana	r.	o.	—	—
Bryophytes				
Barbula fallax	o.	—	r.	—
Brachythecium purum	a.	a.	l.a.	—
B. rutabulum	—	—	r.	r.
B. velutinum	—	—	—	r.
Bryum inclinatum	—	—	f.	—
Camptothecium lutescens	a.	a.	f.	—
Fissidens taxifolius	—	o.	o.	r.
Hylocomium squarrosum	—	—	—	r.
H. triquetrum	l.a.	l.a.	l.a.	—
Hypnum cupressiforme var. elatum	—	l.	—	—
H. cuspidatum	—	—	f.–l.v.a.	a.
H. molluscum	f.	l.a.	l.a.	—
Neckera crispa	—	a.	l.a.	—
Pottia minutula	—	—	r.	—
Trichostomum crispulum	—	—	f.	—
Weisia crispa	—	—	o.	—
Lichen				
Cladonia rangiformis	—	—	r.	—
Total number 145	85	106	92	85
			119	

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ALGAL COLONIZATION AT MUMBLES HEAD

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(*With Plates* 23 *and* 24 *and four Figures in the Text*)

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1. INTRODUCTION AND ACKNOWLEDGEMENTS

The construction of a Grand Trunk Sewage Scheme to serve the area administered by the Swansea County Borough Council was commenced in 1931. The outfall of the main drain was to be situated E.S.E. of Mumbles Head (see Fig. 1), and, in order to lay the outfall pipes, excavation along the foreshore was necessary for a distance of about 800 yards. For the construction of the tunnel through which the pipes were to run, and for the actual placing of the pipes themselves, large quantities of concrete were necessary. The concrete was conveyed to the spot where work was taking place along a narrow-gauge iron rail-track resting on wooden beams supported by concrete piers and walls. At the same level as the narrow-gauge track was a wider one to carry a travelling gantry similarly supported. From November 1932 to August 1935 a series of successively constructed surfaces of concrete, wood and iron became available for algal colonization. The work of demolition in order to restore the foreshore to its original level, and in particular to avoid permanent obstruction across the two sounds which occur at Mumbles Head, was not begun until March 1937, so that the period over which observations were carried out lasted 4½ years. During this period the phases of colonization were observed and the factors determining their succession were studied.

I am greatly indebted to both the Resident Engineer and to the Clerk of Works. In addition to being allowed access at all times to any part of the outfall, I was able to obtain from them many useful data regarding the progress of the work and much general information which was helpful in elucidating ecological problems. In particular, I wish to record my thanks for the data upon which figures 1 and 4 were constructed and for the loan of negatives of Pl. 23, phots. 1 and 2. I wish to express my gratitude also to Commander E. Kirkpatrick-Crockett, the Fisheries Officer of the South Wales Sea Fisheries Committee, for supplying me with information regarding currents and tide-levels at Mumbles Head, and to Lieut.-Commander L. Hugh Milne, R.N., District Inspector of Fisheries, for photographs 3, 4, 5 and 6 which he specially took for me.

2. GEOLOGY OF MUMBLES HEAD

Mumbles Head is a carboniferous limestone promontory consisting of a middle and an outer head. The middle head is cut off from the mainland by a shallow sound (Inner Sound) and from the outer head by another, deeper and wider sound (Outer Sound) (see Fig. 1 and Pl. 23, phot. 1). The sounds have arisen through gradual wave erosion of two initial faults. It will be noticed that the amount of rocky foreshore is much greater on the S.W. side of the Head than on the N.E. side, the latter being the side along which the construction took place. There is also a considerable difference in the aspect of the two sides. Due primarily to glaciation, the rocks on the N.E. side descend steeply into the water, and the foreshore consists largely of boulders, stones and pebbles deposited as the glaciers melted. These are now partially embedded in a sandy mud. On the S.W. side the rocks slope gently to low water, for on this side their form is determined by wave erosion and not by glaciation. Partly because of this difference and partly because of considerable local pollution (see p. 407), the algal flora of the N.E. side is much poorer than on that facing S.W. On the whole of Mumbles Head there are 9 Myxophyceae, 13 Chlorophyceae, 22 Phaeophyceae and 41 Rhodophyceae: of these there are only 6 Myxophyceae, 10 Chlorophyceae, 12 Phaeophyceae and 18 Rhodophyceae on the N.E. side.

3. TIDAL AND OTHER CONDITIONS AT MUMBLES HEAD

The incoming tide wave advances up the Bristol Channel from a south-westerly direction, passing Mumbles Head at the rate of 3 knots during spring tides and 2 knots during neaps. Owing to the gradual narrowing of the

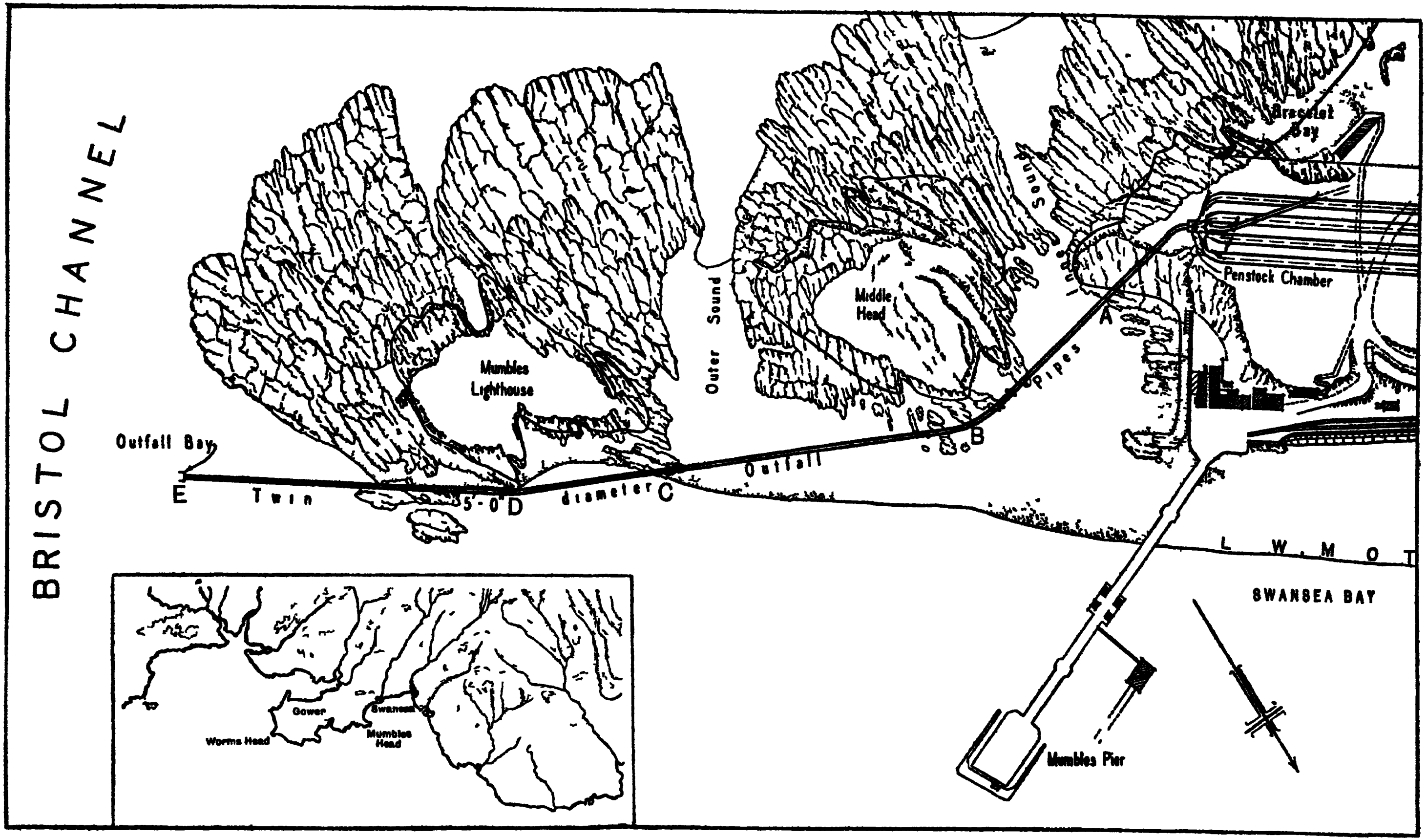


Fig 1 Mumbles Head General plan of outfall along N N E side of Middle and Outer Head, and across Inner and Outer Sound. Inset, map of part of South Wales coast showing position of Gower and Mumbles Head

Channel, one wave becomes superimposed upon another, adding to the height of the crest, so that at spring tides the height of the water (i.e. rise of spring tide) is 27¼ ft. (8·4 m.). High water at full and change of moon is at 6.16 p.m., low water of spring tides is therefore about midday and midnight, allowing only one maximum exposure during which the light is at its highest intensity. In addition to these more general effects, there are five peculiarities about the tidal wave at Mumbles Head which are of ecological importance.

(1) The trend of the incoming (flood) tide along the coast of South Gower is along the shore with two eddies at Oxwich Bay and Port Eynon Bay. From Mumbles Head the tide sets towards Swansea and Neath, its direction and rate of flow being affected by the drainage channels leading from Swansea Docks (these channels cause eddying currents). The outgoing (ebb) tide on the other hand flows in and around Swansea Bay, joining a northward eddying stream near Port Talbot and a westward one near Neath, and then circling and setting around Swansea Bay towards Mumbles Head (see Fig. 2). This leads to a fairly constant swirl of water around the headland and through the sounds (actually it is this factor which has been made use of in connexion with the placing of the sewage outlet).

(2) Owing to the eddy in Swansea Bay, the actual time of an ebb tide on the Swansea Bay side of Mumbles Head is 9 hr.; as a result of this a portion of the Bay near Mumbles Head is prone to deposit by flotsam.

(3) The main ebb tide flows swiftly by, averaging 3–4 knots, and during spring tides or after heavy rainfall, which brings in freshings from rivers and streams, it develops a strong race which, owing to the effect of a shoal (the Mixon shoal) near the Head, leads frequently to heavy seas especially with E., S. or W. winds. In addition to the frequency of heavy seas, a rapid sweep of water occurs over the rocky ledges beyond the outer Head: this is caused by a partially sunken rock about 200 yards out from low water of ordinary tides, with a deep channel between it and the base of the rocky ledge. Hence the water near the Head is both turbulent and swiftly flowing, well aerated and constantly changing.

(4) During warm and calm periods in summer and early autumn, owing to the very extensive area of sand and sandy mud uncovered in the very shallow Swansea Bay, the temperature of the water, especially of a tide coming in late in the day, is appreciably above the average for sea water at that time. Similarly in winter it is correspondingly colder (ice blocks were abundant along the bay in December 1938 and January 1940). As will be pointed out later (see p. 426), when such periods coincide with a period of copious or extensive fruiting of certain marine algae, phases of succession are considerably influenced.

(5) Both the frequently turbulent and always swiftly flowing water around the Head, and the calmer, more sheltered water of the Swansea Bay side of the Head may be seriously affected by pollution. In one of the reports of the Fisheries Officer the following passage occurs: "The River Tawe is dreadfully

polluted and experiments carried out over the dumps from dredging confirm this...the effect of oily residues from roads, garages and entering sewers is most apparent when the silt is 'washed' and then held in suspension loosely, when the surface is covered with a thick oily film....Fish are thus thin from lack of food; they do not develop or fatten: shellfish and jellyfish are flaccid from the effects of pollution....Fish appear prone to parasites in this area." There is strong reason to believe that this pollution is a potent factor influencing both algal and animal communities particularly in regions A–C (see Fig. 1 and also pp. 427, 429).

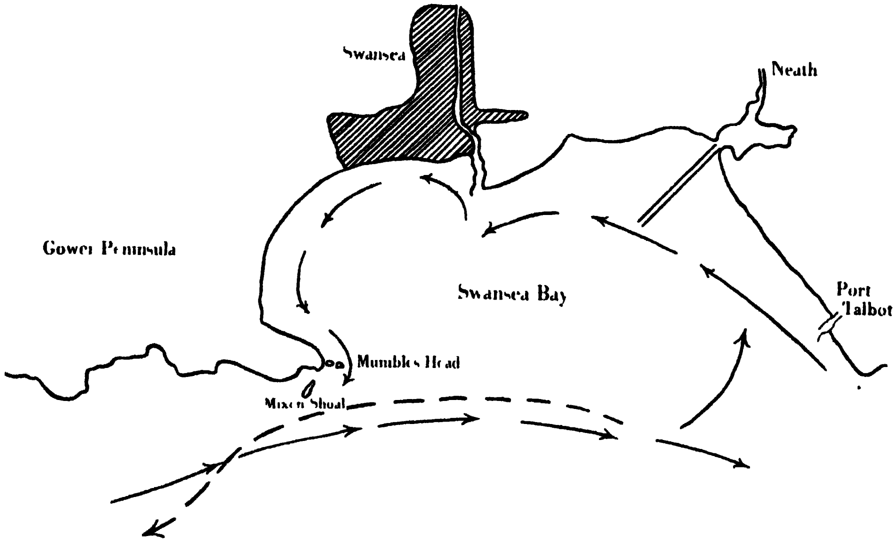


Fig. 2. Shows only tidal currents near Swansea Bay. The broken line shows the set of ebb tide outside the bay.

4. TYPES OF SUBSTRATA COLONIZED

In the geological and hydrographical setting described above, new surfaces of concrete, wood and iron were made available for colonization by such marine algae and animals as normally occur within the bathymetric range of the structures erected. In order to obtain data as comprehensive as possible, observations were recorded according to the following scheme:

A. *Concrete walls and piers.*
  (1) Vertical surfaces: (*a*) exposed, facing E.S.E.; N.N.E.; W.N.W.; S.S.W.
    (*b*) protected, facing E.S.E.; N.N.E.; W.N.W.; S.S.W.
  (2) Horizontal surfaces, facing upward or downwards.

B. *Cable posts.*
  Seventeen of these were erected and data obtained for (*a*) exposed surfaces, (*b*) sheltered surfaces, (*c*) level above or below ordnance datum.

C. *Iron rail-track.*
  (i) Vertical surfaces facing N.N.E. and S.S.W.
  (ii) Horizontal surfaces.
D. *Iron pipes* (conveying steam under pressure).
  (i) Upper surface.
  (ii) Lower surface.
E. *Wooden piles or beams.*
  (i) Vertical surfaces: (*a*) exposed, facing E.S.E.; N.N.E.; W.N.W.; S.S.W. (*b*) Protected, facing E.S.E.; N.N.E.; W.N.W.; S.S.W.
  (ii) Horizontal surfaces, facing upwards or downwards.
  (iii) Various crosspieces involving varying angles of slope.
  (iv) Level above or below ordnance datum.
F. *Other new surfaces.*
  (i) Patches of concrete due to leakage from trucks.
  (ii) Ballast stones and packing for sleepers.
  (iii) Temporary artificial pools due to local clearance.

5. RELATION OF SURFACES TO TIDE LEVELS

Before setting out the main features of the progressive colonization of the above surfaces, it is important to establish their positions with reference to tide levels. The value of data of this kind has been recently stressed by Colman (1932–3), Grubb (1936) and Zaneveld (1937). Adopting Colman's scheme, the following tide levels obtain at Mumbles Head:

	Feet above/below ordnance datum
E.H.W.S., extreme high water spring tides	+16·6 (=5·06 m.)
M.H.W.S., mean high water spring tides	+14·5 (=4·42 m.)
M.H.W.N., mean high water neap tides	+ 7·08 (=2·16 m.)
E.H.W.N., extreme (lowest) high water neap tides	+ 5·6 (=1·71 m.)
M.S.L., mean sea-level	− 0·25 (=0·076 m.)
E.L.W.N., extreme (highest) low water neap tides	− 4·1 (=1·25 m.)
M.L.W.N., mean low water neap tides	− 5·72 (=1·74 m.)
M.L.W.S., mean low water spring tides	−13·28 (=4·05 m.)
Chart datum	−14·0 (=4·26 m.)
E.L.W.S., extreme low water spring tides	−16·2 (=4·94 m.)

From the above figures it will be seen that:

(*a*) The average rise of a spring tide is 27·78 ft. (=8·47 m.)
(*b*) The extreme rise of a spring tide is 32·80 ft. (=9·99 m.).
(*c*) The average rise of a neap tide is 12·80 ft. (=3·90 m.).
(*d*) The least rise of a neap tide is 9·70 ft. (=2·96 m.).

The rail-track bearing the gantry and the narrower rail-track for the trucks carrying concrete were roughly 3 ft. above O.D. from the point C (see Fig. 1) outwards, but fell to 1 ft. (0·31 m.) above O.D. from C to B. Since all the concrete work and wooden beams were below the level of the rails, almost the whole of the colonization took place at a level below E.H.W.N. Thus the algae were always covered at high water. The lower limits, which correspond to the general shore level dropped from E.L.W.N. (B to C) to M.L.W.S. (nearing E).

Using Zaneveld's classification (1937) the region investigated would fall into the medio-littoral and baso-littoral belt.

To this general statement regarding the upper and lower limits of the main region of colonization, there were three exceptions. First, the gantry and crane, which was kept mainly between C and E. Secondly the cable posts positioned at various points between the mainland and the outlet at E (see Fig. 1). Thirdly the staging for the concrete mixer near B and the stage for the gantry at D. The upper parts of these were well above the level of E.H.W.S. and consequently could be colonized by algae which normally occupy belts or zones above E.H.W.N., i.e. the ultra- and supra-littoral belts of Zaneveld.

6. ALGAE AND ANIMALS CONCERNED IN THE COLONIZATION

The list below represents the limited number of algae taking part in colonization (see also p. 432).

MYXOPHYCEAE: 1. Lyngbya aestuarii Leibm.
2. Phormidium sp.
CHLOROPHYCEAE: 3. Ulothrix flacca Thur.
4. U. speciosa Kütz.
5. Urospora isogona Batt.
6. Enteromorpha minima Näg.
7. E. compressa Grev.
8. E. compressa var. nana J.G.Ag.
9. E. intestinalis Link.
10. Ulva lactuca L.
PHAEOPHYCEAE: 11. Pylaiella littoralis Kjellm.
12. Ectocarpus spp.
13. Pelvetia canaliculata Dcne. & Thur.
14. Fucus vesiculosus L.
15. F. spiralis L.
16. F. serratus L.
RHODOPHYCEAE: 17. Bangia fusco-purpurea Lyngb.
18. Porphyra umbilicalis (L.) Ag.
19. P. umbilicalis var. linearis Grev.
20. Callithamnion byssoides Arn.
21. Ceramium rubrum Ag.
22. Chondrus crispus Stackh.
BACILLARIOPHYCEAE: 23. Schizonema spp.

In addition the following marine animals made their appearance:

1. Dyanema pumila
2. Campanularia flexuosa
3. Pomatoceros triqueter
4. Teredo sp.
5. Actinia equina
6. Littorina littoralis
7. Mytilus edulis
8. Balanus balanoides
9. Patella vulgata

7. PROGRESS OF THE CONSTRUCTION

The first stage, which lasted from the spring of 1932 to August of that year, consisted of the erection of wooden piles across the inner sound (see Pl. 23, phot. 1). Strengthened by various cross-beams and stays, they carried large wooden beams upon which rested a rail-track for a travelling crane, and also a narrow-gauge rail-track for trucks taking material required for the erection and fitting of a concrete mixer on the middle head (extreme left of Pl. 23, phot. 1). It will be seen from the photograph that, apart from the iron rail-tracks, the surfaces exposed for colonization were entirely of wood. The normal condition of the inner sound is clearly to be seen—in the foreground is sand, next come small angular stones, with occasional larger boulders appearing to the right, covered with *Fucus vesiculosus*. Normally the vegetation of the sound is sparse owing to the very unstable nature of the greater part of the substratum. Roughly speaking, the level of the rail-track is that of M.H.W.S., whilst the foreshore is at M.S.L., colonization therefore taking place between these tide levels. This first phase in the progress of the work may be said to have ended in August 1932 when the concrete mixer was finished and stage B erected. Soon after that date the whole structure was dismantled.

The second phase extended from October 1932 to November 1933, when across the outer sound a rail track was laid down from B to C. At the beginning of the track—near B—the foreshore is fairly level and concrete was used to support the rails, but towards the middle of the sound, where the foreshore drops slightly, the track was supported upon a solid palisade of vertically placed sleepers. As the region near C was approached it became necessary to construct concrete piers and walls to give adequate support. The level of this rail-track was about 1 ft. above O.D., and thus just a little above M.S.L. Trucks filled with concrete travelling along this track were apt to jolt and spill small quantities which fell on to the small angular stones which—as in the case of the inner sound—form the greater part of the substratum from B to C. The surfaces available for colonization were therefore of wood, iron and concrete, extending from 1¼ ft. above M.S.L. to 1 ft. above E.L.W.N.—a narrow vertical zone rarely exceeding 4 ft. in depth. In addition to the rail-track, a stage for pumps and switchboard was erected in December 1933, just a little to the left of C (see Fig. 1).

The third phase, which was by far the most interesting from the ecological standpoint, began in November 1933 and continued until August 1935, when, month by month as weather and tides permitted, the outer part of the work was undertaken from C to E. As will be seen from Pl. 23, phot. 2, and Pl. 24, phot. 3, the general level of the shore drops at first gradually, later more rapidly, and massive piers and walls of concrete were erected to carry the rail-track for gantry and trucks. After the final construction of the outlet was completed, the whole structure was left for 18 months before the work of demolition began in March 1937. Demolition continued until September 1937 by which date everything erected had been dynamited and the foreshore left at its original level, but with the addition of many thousands of small pieces of concrete strewn over the shore for a distance of 20–30 yards on either side of the original track. For almost four years, therefore, concrete, wood and iron surfaces varying in aspect, degree of shelter and angle of slope were available for colonization by marine algae and animals which flourish between M.S.L. and M.L.W.S.

As well as the erections above referred to, additional and somewhat different new surfaces were provided by the erection of (*a*) cable posts for carrying electric cables and (*b*) wooden stages for pumps, machinery, gantry and switchboard. The cable posts, of which there were 21 in all, were of the telegraph-pole type (see Pl. 23, phot. 2) and were erected at about the same time as the rail-track in the corresponding position. From B to C there were eight posts erected between February and December 1933; from C to D five posts were erected between January and May 1934, and between D and E eight posts were put up between June 1934 and April 1935. The dates of completion of the three wooden stages at B, C and D were 8 August 1933, 12 December 1933 and 3 May 1934 respectively. Both cable posts and stages were taken down between March and September 1937.

8. THE PERIODS AVAILABLE FOR COLONIZATION

These are best set out in the form of a table:

Region	Substratum	Length of time available for colonization	Season
A–B	Wood piles Wood beams Iron rail-track	3–9 months	Late winter Spring Summer
B–C	Concrete bed Wood palisade Wood beams Concrete piers and walls Iron rail-track	4–5 years	All seasons
C–D	Mainly concrete piers and walls Wood beams Iron rail-track	3¼–4 years	Late autumn Winter Spring
D–E	Mainly concrete piers, walls and flat surfaces Wood beams Iron rail-track	2½–3¼ years	All seasons

9. PHASES OF COLONIZATION

(*a*) *Pioneer communities*

The nature of the pioneer community depends upon (*a*) the season of the year and (*b*) the tide level. Most marine algae have well-defined periods of fruiting and in the case of several of the Chlorophyceae and Rhodophyceae, the sexual and asexual reproductive bodies mature and are liberated at different periods of the year. Thus *Enteromorpha compressa* produces gametes in summer and zoospores in winter, spring and autumn: *Porphyra umbilicalis* produces gonidia in early autumn, and carpospores from winter to summer. It is evident that the chance of colonizing any newly constructed surface will depend upon the availability of spores. As will be clear from p. 409 only a few of the algae whose spores were being emitted at any particular time actually did take part in the colonization. Reasons underlying this limitation will be considered later (see p. 432). The results of observations made during all three phases of construction and upon all types of substrata were so closely similar that they may be summarized as follows:

(*a*) *Pioneer communities during spring* (March–May).
  (1) M.H.W.N. to M.S.L. *Ulothrix flacca*, *U. speciosa*, *Urospora isogona*, together with a little *Ulva lactuca* and *Porphyra umbilicalis*.
  (2) M.S.L. to M.L.W.S. *Ulva lactuca*, *Porphyra umbilicalis*, *Enteromorpha compressa*, together with *Balanus balanoides*.
(*b*) *Pioneer communities during summer* (June–August).
  (1) M.H.W.N. to M.S.L. *Enteromorpha minima*, *E. compressa*.
  (2) M.S.L. to M.L.W.S. *Enteromorpha compressa*, *E. intestinalis*, *Porphyra umbilicalis*, *Campanularia* sp.
(*c*) *Pioneer communities during autumn* (September–November).
  (1) M.H.W.N. to M.S.L. *Porphyra umbilicalis* f. *linearis*, *Enteromorpha compressa*.
  (2) M.S.L. to M.L.W.S. *Enteromorpha compressa*, *Pomatoceros triqueter*.
(*d*) *Pioneer communities during winter* (December–February).
  (1) M.H.W.N. to M.S.L. A little *Porphyra umbilicalis* and *Enteromorpha compressa*.
  (2) M.S.L. to M.L.W.S. *Porphyra umbilicalis*, *Enteromorpha compressa*.

Stating these observations in general terms, the spring is characterized by the appearance of a thick felt-like mat of filamentous green algae which grow on iron, wood and concrete, covering the surfaces in a zone about 4 ft. (1·3 m.) in depth, rarely extending above M.H.W.N. and best developed from 2 to 3 ft. (0·6–0·9 m.) below that level. Towards M.S.L. occasional patches of *Ulva lactuca* and scattered local communities of *Porphyra umbilicalis* occur. Below M.S.L. these two algae become more prominent, *Ulva* being especially noticeable in any small pools or damp sheltered regions. None of the filamentous algae occur at such levels, but *Enteromorpha compressa* is often quite abundant on wood (far less so on concrete at this season of the year) and towards May the spat of *Balanus* becomes prominent on concrete. By June most of the mats of filamentous algae have disappeared, and in their place, and in similar zones on newly completed surfaces, *Enteromorpha minima* appears, whilst below M.S.L. considerable growths of *E. intestinalis* occur. This alga is fairly abundant in neighbouring rock pools between E.H.W.N. and M.H.W.S. Since there are so few plants of this species below these levels, it appears likely that the spores which germinate on newly erected surfaces are derived from the pool-inhabiting plants and that their germination at levels so much lower is an additional example of "algal migration" to which attention has recently been drawn by Knight & Parke (1931) and Rees (1934). A migration in the reverse direction is shown by *E. compressa*. Whilst in spring it is more abundant below M.S.L. than above, in summer, autumn and winter its spores germinate to a far greater extent above M.S.L. During summer, along with *E. minima*, it grows copiously as a pioneer on new surfaces between M.H.W.N. and M.S.L. Throughout the summer new crops of *Porphyra umbilicalis* are appearing (see p. 430) and, together with *Enteromorpha intestinalis*, it is the dominant pioneer alga of this season. During the summer the pools become invaded by *Campanularia* (see also p. 424).

Towards September, *Enteromorpha compressa* begins to produce zoospores copiously and in October and November is a prominent new arrival above M.S.L., whilst towards November *Porphyra umbilicalis* f. *linearis* forms dense local sheets on all types of substrata. At much lower levels—M.L.W.S. to M.L.W.N.—*Pomatoceros triqueter* becomes prominent. During late autumn and throughout the winter, *Porphyra umbilicalis* f. *linearis* is practically the only pioneer alga, though there are occasional and spasmodic intrusions by *Enteromorpha compressa* both above and slightly below M.S.L.

It has been mentioned above that these pioneer communities are to be found developing upon all types of substrata. Neither the aspect nor the angle of slope appear to have any marked effect, sporelings establishing themselves on any available surface. But within a few weeks factors of the environment, including competition, begin to influence the development of the communities and the succeeding stages are markedly different under differing conditions. The factors which appear to determine succession are:

(*a*) The nature of the substratum.
(*b*) The tide level.
(*c*) The aspect (particularly the degree of shelter).
(*d*) The angle of slope.
(*e*) Competition between pioneer algae and later arrivals.
(*f*) Competition between pioneer algae (and those of the early stages in succession) and certain marine animals.

These factors are so closely linked together that it is impossible to deal with the influence of each one separately, but it is fairly clear that the first two are of greatest importance. It is, however, largely a matter of convenience in presentation that the treatment of succession is divided primarily upon the basis of the nature of the substratum.

(*b*) *Succession*

(i) *Iron substrata.*

There were several different kinds of iron substrata. Two of them (the iron rail-tracks and the steam-pressure piping) occur at about M.S.L. from B to E. The others vary considerably with reference to tide level. Thus on many of the cable posts there were iron steps from M.H.W.N. to M.L.W.N. The framework of the travelling crane which was kept, when not in use, on the platform D, exposed surfaces from M.S.L. to E.H.W.S. Finally, along the shore there was a good deal of iron junk consisting of iron pipes, rods, chains, boxes and sheets which had been cast aside. In general, the iron was poorly colonized owing to the flaking off of rust. During periods of very rapid and copious spore production, e.g. the *Ulothrix* phase in spring or the *Enteromorpha compressa* phase in late summer, whole surfaces would become covered temporarily by young sporelings, but later the algal growth would become scanty. Newly bared surfaces formed by the falling off of rust flakes were sometimes temporarily recolonized by sporelings, older surfaces continuing to bear scattered tufts of *Enteromorpha* or *Porphyra.* On the rails themselves, algal growth was confined largely to the lower flange and the web. An interesting feature which was so much in evidence as to be considered a general characteristic of the distribution on these rails, was that whilst *Enteromorpha compressa* was frequently found growing on vertical, and on the underside of horizontal, surfaces, *Porphyra umbilicalis* grew only on surfaces practically horizontal. On the wooden beams supporting the rails, however, both species grew plentifully on vertical and horizontal surfaces.

A similar difference in distribution was noticeable during the second and third year when an invasion of Fucaceae took place. *Fucus vesiculosus* was largely confined to the vertical web, whereas the *F. serratus* was found only on the lower flange. At no time did *Balanus* spat settle on the rails, nor in fact upon any of the other iron surfaces. The only other colonizer of iron rails was *Ceramium rubrum*, local patches of which, as well as occasional isolated plants, were found on the lower flange.

The iron pipes, partly because of the round surface and partly because of an inferior resistance to rust, were very poorly colonized until the invasion of the Fucaceae in the third year. Both *Fucus vesiculosus* and *F. serratus*, because their gradually widening holdfasts gave protection to the iron surfaces, grew in dense aggregates covering both rails and pipes to the exclusion of all other algae. Even in the fourth year there was no trace of any subvegetation in the *Fucus* communities.

On many of the iron steps fitted to the cable posts, and on the iron framework of the travelling crane, a definite zonation was to be seen. At about M.H.W.N. *Enteromorpha minima* formed a dense clinging growth, which was gradually replaced at E.H.W.N. by *E. compressa* f. *nana*, and toward M.S.L. by a mixture of *E. compressa* and *Porphyra umbilicalis* with the latter definitely dominant below M.S.L. Both *E. minima* and *E. compressa* belong to the group termed pseudoperennials by Knight & Parke (1931) and the pioneer community which they establish is continued by regeneration and sporing until the invasion of the Fucaceae for which they have prepared the way (see p. 434). In the second and subsequent years these pioneer communities are replaced by *F. vesiculosus*, *F. spiralis* and *Pelvetia canaliculata* at the appropriate level.

With regard to the later phases of colonization of the assorted iron junk, most of which being fairly light was moved about by rough seas, no clear sequence could be followed, except that each year the spring invasion of *Ulothrix* and *Urospora*, the late summer invasion of *Enteromorpha compressa* and the winter invasion of *Porphyra umbilicalis* f. *linearis* often created dense temporary coverings which within a few months had disappeared through the flaking off of rust.

Summing up, the original pioneer communities and the phases of succession on iron substrate were patchy and discontinuous, but they served to emphasize locally the general trend which was so well marked on concrete surfaces. It is noteworthy that at no time did any animal community nor any individual animal establish itself on iron.

(ii) *Wood substrata.*

As in the case of the iron substrata, the surface of wood exposed for colonization may be divided into two main categories. First, wood so placed as to provide surfaces at different tide levels. To this group belong (*a*) the wooden piles and beams across the inner sound; (*b*) the wooden framework of the three stages at B, C and D; (*c*) the wooden palisade across part of the outer sound and (*d*) the cable posts. Secondly, wood left for a considerable period at the same tide level, as for example the beams upon which the iron rail rested, together with occasional sleepers or beams at right angles to the main track. Constructed at various periods from November 1933 to August 1935, and remaining intact until the final demolition in September 1937, they provided surfaces available for colonization at about M.S.L. for 2-4 years.

The wooden piles and cross-beams erected over the inner sound (see Pl. 23, phot. 1) were in existence only for a short period during the spring and summer of 1932 and were colonized only by pioneer communities of *Ulothrix*, *Urospora*, *Enteromorpha minima* and *E. compressa* (cf. p. 412).

The framework of the three stages at B, C and D, constructed almost entirely above M.S.L., presented surfaces for colonization extending from 3 to 5 years. The succession following upon the usual pioneer communities was the same in each case. From M.H.W.S. to M.H.W.N. *Enteromorpha minima* remained the sole colonizer maintaining continuity by (*a*) spores, (*b*) proliferation and detachment. Very occasionally a few threads of *Ulothrix* spp., *Urospora* and *Bangia fuscopurpurea* were to be found at this level in spring and early summer.

From M.H.W.N. to M.S.L., *Enteromorpha compressa* was dominant, but increasingly replaced by *Porphyra umbilicalis* just above M.S.L. The winter and spring invasions of this alga led to temporary joint communities, but towards autumn *Enteromorpha compressa* would become dominant again, partly because of the death of the *Porphyra* plants, partly because of new sporelings. It was not until the third year after their erection that the framework of each of the stages was colonized by Fucaceae, *Pelvetia canaliculata*, *Fucus vesiculosus* and a small quantity of *F. serratus*, each in its respective zone rapidly replaced the *Enteromorpha*, which however remained in diminished quantity

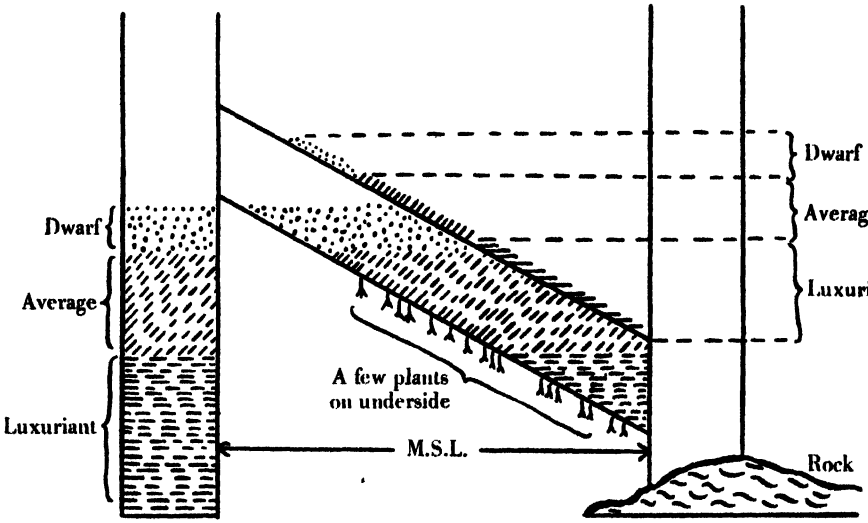


Fig. 3. Showing upward extension of *Fucus vesiculosus* on cross-beams.

as a subvegetation to the Fucaceae. Certain surfaces which were too exposed for the Fucaceae, or were in some other way unsuited to their growth, remained throughout the period colonized jointly by *Enteromorpha* and *Porphyra*. The only other algae found were *Ulva lactuca* and *Bangia fuscopurpurea*. Neither *Enteromorpha compressa* nor *Porphyra umbilicalis* appear to be affected by aspect or angle of slope, but the effect of these factors is well seen in the distribution of the Fucaceae. Thus *Pelvetia* will not grow on absolutely vertical surfaces, but it can withstand considerable exposure to wave action. *Fucus spiralis* was completely absent from the woodwork. *F. vesiculosus*, though able to grow well on vertical surfaces, reaches luxuriance only on gently sloping ones. A very interesting example of the effect of slope upon the occurrence, distribution and luxuriance of *F. vesiculosus* was afforded by several cross-beams on the stages at B and C: these beams were at an angle of about 30° (see Fig. 3).

On the upper surface of the cross-bar there was, for each of the three zones of dwarf, average and luxuriant plants, an upward extension of from 2 to 2½ ft. (60–75 cm.), whilst on the lower surface of the beam only a few scattered dwarf individuals were found. It is obvious that the chances of successful germination on the lower surface are few owing to gravity, but although an upward extension of the upper limit of the zone of *F. vesiculosus* on a rocky shore is occasionally found (Rees, 1931) when the rocks slope very gently and the coast is sheltered, a marked change of limit as illustrated above—under the same general ecological conditions—must result from the effect of the angle of slope of the substratum. Spores will alight and find temporary lodgement in the minute crevices of the wood surface at all levels, but the sporelings which develop towards the upper limits of the normal belt occupied by *F. vesiculosus* are less healthy and are consequently more easily torn away from vertical surfaces by wave action. In the struggle between surf action and the tenacity of the holdfast mechanism, plants which are depauperated will be able to survive only upon more gently sloping surfaces, where in addition to a more firm attachment to the wood, they grow in such profusion as to provide mutual protection. It may be noted here that on vertical or steeply sloping surfaces of both rock and wood there is a more sudden transition between healthy and depauperate plants than is to be found on flat or gently sloping surfaces. Whilst the sharpness of the contrast is obviously due in the main to the more rapid change in tide level when viewed on a vertical surface, it is evident that retention of water by overlying thalli when the tide is out is also an important factor. On the vertical wooden posts the plants of *F. vesiculosus* near the upper limit are always very dry for several hours during spring tides whereas those growing on the sloping beam are moist even on hot dry days. Finally, in this connexion, the absence of *F. spiralis* undoubtedly allows a more gradual upward extension than is the case in regions where these two Fuci are in competition (cf. Zaneveld, 1937).

The effect of degree of exposure to surf action can be studied both on the cable posts and upon some portions of the woodwork of the stages. The prevailing wind is south-westerly and most storms come from that direction. Consequently posts and portions of the stages protected by the middle and outer head are sheltered from storms. Cable posts set up across the outer sound or beyond the outer head are often devoid of Fucaceae, but those in the shelter of the outer head are clothed in the second and third year with dense hanging festoons, more particularly of *F. vesiculosus*, but also of *F. serratus* near their base. Similarly, parts of the stages which project beyond the region of protection afforded by the middle and outer heads are either bare or have a far scantier growth of Fuci than those fully protected.

The main phases of colonization of the cable posts are summarized in the accompanying table. The four posts selected are representative of (*a*) different times of erection influencing the pioneer communities, (*b*) different degrees of exposure to wave action influencing the succession. The following abbreviations are used in this table:

oc.	occasional	fr.	frequent
ab.	abundant	E.	*Enteromorpha*
U.	*Ulothrix*	F.v.	*Fucus vesiculosus*
F.s.	*Fucus serratus*		

The *Porphyra* referred to is *P. umbilicalis*, and the *Ulva* is *U. lactuca* and the *Ceramium* is *C. rubrum*.

The following are the most noteworthy features of the colonization of the cable posts:

(1) Except for a few scattered *Balanus* and occasional patches of *Campanularia* at low-water mark, these posts, in common with other wood substrata, bore no animal communities.

(2) There was frequently a marked contrast between the N.N.E. (sheltered) and the S.S.W. (exposed) side (cf. post no. 6, second year and third year, M.H.W.N. to M.L.W.N. and posts nos. 17 and 20, second and third year M.H.W.N. to M.L.W.N.).

(3) Both *Enteromorpha minima* and *E. compressa* extended to a higher level on the posts than was the case on piles. It is difficult to find a satisfactory explanation of this since the influence of spray appears to be the same in each case.

(4) The bareness of the region between M.L.W.N. and M.L.W.S. is due to constant trituration of the base of the poles by small stones, pebbles and gravel.

(5) The general sequence, allowing for such factors as exposure to wave action and tide-level, is that both *E. compressa* and *Porphyra umbilicalis* may, by sporing, continue into a second or third year the pioneer communities which they constitute, but that usually they are replaced by Fucaceae which occur as sporelings in the second year and adult plants in the third.

(6) The greater bareness of the posts from D to E is due to the swirling and turbulent character of the water in this region, as well as to exposure to wave action.

The main interest of the horizontal wooden beams and sleepers lies in the contrast which they provide with the iron rail-track on the one hand and the concrete piers and walls on the other. Owing largely to the inability of several algal and animal species to gain a foothold on wood, the succession is a fairly simple one, comparable to that of the iron rail. The pioneer algae produce in due course their spores or gametes. Plantlets arising from these compete with each other and with parent plants with two interesting results.

(*a*) If one particular alga is sporing freely, especially during a period of calm weather, its sporelings develop rapidly and dominate the next phase. Thus for instance in January–February 1935, when the "*linearis*" form of *Porphyra* was producing abundant carpospores, the beams were found in April

Colonization of cable posts

No. of post ...	6		12		17		20	
Position ...	Outer Sound		Below Outer Head		Beyond Outer Head		Near Outfall (E)	
Date of erection ...	October 1933		May 1934		August 1934		January 1935	
	Pioneer communities		Pioneer communities		Pioneer communities		Pioneer communities	
Aspect ...	N.N.E.	S.S.W.	N.N.E.	S.S.W.	N.N.E.	S.S.W.	N.N.E.	S.S.W.
M.H.W.S. to M.H.W.N.	oc. Porphyra	oc. Porphyra	U. flacca U. speciosa E. minima	U. flacca U. speciosa E. minima	E. minima oc.	E. minima E. compressa	oc. Porphyra	oc. Porphyra
M.H.W.N. to M.S.L.	oc. E. compressa ab. Porphyra	oc. E. compressa ab. Porphyra	E. compressa	E. compressa U. flacca	Bare	E. intestinalis	fr. Porphyra	fr. Porphyra
M.S.L. to M.L.W.N.	fr. Porphyra	fr. Porphyra	A few Ulva	oc. Porphyra A few Ulva	Bare	Bare	oc. Porphyra	Bare
M.L.W.N. to M.L.W.S.	Bare	Bare	Bare	A few Balanus	Bare	Bare	Bare	Bare
	Second year		Second year		Second year		Second year	
	N.N.E.	S.S.W.	N.N.E.	S.S.W.	N.N.E.	S.S.W.	N.N.E.	S.S.W.
M.H.W.S. to M.H.W.N.	oc. E. compressa	oc. E. compressa	A few sporeling Pelvetia	A few sporeling Pelvetia	E. minima oc.	Almost bare	oc. Porphyra	Bare
M.H.W.N. to M.S.L.	oc. E. compressa oc. Porphyra A few Ulva	Bare	ab. sporeling F.v.	ab. sporeling F.v.	A few sporeling F.v.	Bare	fr. Porphyra A few F.v.	A few F.v.
M.S.L. to M.L.W.N.	oc. Porphyra	A few Porphyra	oc. F.v. oc. F.s. oc. Ulva	oc. F.v. oc. F.s. Ulva	Bare	Bare	Bare	Bare
M.L.W.N. to M.L.W.S.	Bare	Bare		Balanus	Campanularia	Campanularia	Bare	Bare
	Third year		Third year		Third year		Third year	
	N.N.E.	S.S.W.	N.N.E.	S.S.W.	N.N.E.	S.S.W.	N.N.E.	S.S.W.
M.H.W.S. to M.H.W.N.	oc. E. compressa	Bare	oc. Pelvetia	oc. Pelvetia	E. minima A few E. compressa	E. compressa oc.	oc. Porphyra	Bare
M.H.W.N. to M.S.L.	Thick festoons of F.v.	A few scattered F.v.	Thick mats of F.v. and oc. F.s.	Thick mats of F.v. and oc. F.s.	fr. F.v.	Bare	oc. F.v. A few Ceramium	Bare
M.S.L. to M.L.W.N.	Thick festoons of F.v.	A few scattered F.v.	Thick mats of F.v. and oc. F.s.	Thick mats of F.v. and oc. F.s.	A few Ulva	Bare	oc. F.v. A few Ceramium	Bare
M.L.W.N. to M.L.W.S.	A few Ulva	A few Ulva	ab. sporeling F.s.	Ulva ab. sporeling F.s.	oc. F.s.	Bare	Campanularia	Campanularia

to be densely clothed by tiny plantlets of *Porphyra* occupying bare patches or places previously occupied by decaying or dead pioneer algae. Under these circumstances the spring *Ulothrix-Urospora* phase was poorly developed, having very little bare surface to colonize. But in a similar period in 1936, owing to much rougher weather (and possibly also to less abundant sporing by *Porphyra*) only a few new *Porphyra* plants developed, with the result that the later *Ulothrix-Urospora* phase covered the beams with sheets of filaments lasting until early summer, when they were replaced by *Enteromorpha compressa*.

(*b*) In the absence of abundant sporing by any one alga and periods of calm weather, the community developed during the second year tends to be a mixed one of *E. compressa*, *E. intestinalis*, *Ulva lactuca* and *Porphyra umbilicalis*.

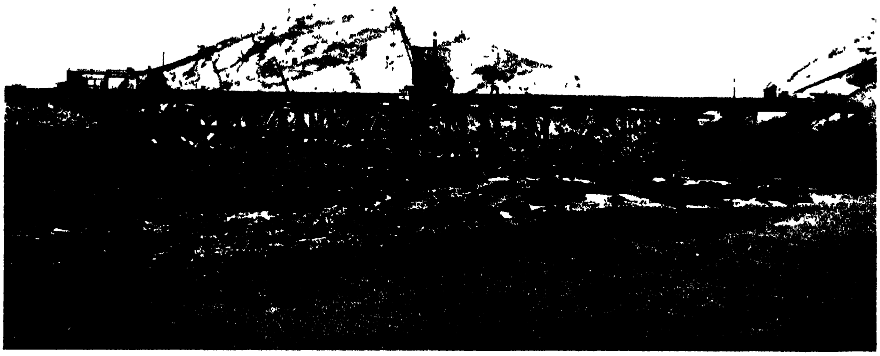
The beams are too small to show any effect of shelter or exposure with reference to their N.N.E. or S.S.W. surfaces, and except that the underside (where free) is but little colonized, angle of slope does not appear to be important.

Unlike the cable posts (which bore communities of sporeling Fucaceae in the second year) *Fucus vesiculosus* and *F. serratus* did not appear until the third year after erection. Both were then found growing plentifully, but as is elsewhere so frequently the case, vertical sides were colonized almost wholly by *F. vesiculosus*. During the third year occasional tufts of *Pylaiella littoralis*, *Ectocarpus confervoides* and other indeterminate species of *Ectocarpus* were to be found, together with a few scattered tufts of *Ulva lactuca*, especially on the under surface. No animals appeared to be able to settle on the beams, but in the third year it was evident that wood-boring species were beginning to attack them in parts. Throughout the phase during which sporelings of *Fucus vesiculosus* and *F. serratus* were developing into adult plants, *Enteromorpha compressa* and *E. intestinalis* were to be found as a subvegetation.

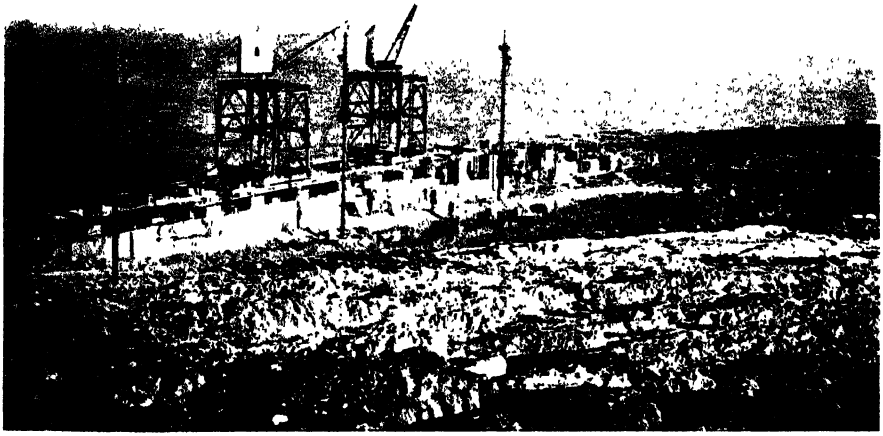
Finally, the wood palisade supporting the rails near B did not differ materially from the beams either in the nature of the pioneer communities or in the subsequent succession to the *Fucus* phase. Marine boring animals (*Teredo* sp.) were, however, more abundant, and in May 1936 *Balanus* spat settled, but remained quiescent, and failing to develop was washed away by rough seas late in that month.

(iii) *Concrete substrata.*

Before considering the sequence of colonization it is necessary to give a fuller description of the nature of the various concrete surfaces. In the first place there were two parallel series of concrete piers, constructed at intervals of 6–14 ft. (2–4·7 m.) beginning at C and continuing to the outfall at E. These were rectangular in shape with a plinth at their base, their height varying with the level of the foreshore. Pl. 23, phot. 2 shows them in process of construction near E. Between the piers concrete walls were built, again in two parallel



Phot. 1. Inner Sound, region A–B, showing foreshore, rail-track beams and piles, the latter dark with growths of *Enteromorpha minima* and *E. compressa*.



Phot. 2. Region between D and E, showing erection of piers and walls of increasing height as level of foreshore falls. Three cable-posts also shown.

series (see diagrams 4*a* and 4*b*). The tops of the walls were from 1 ft. to 1 ft. 6 in. (30–45 cm.) lower than those of the piers, and like them the walls were of varying height above the shore (see Pl. 24, phots. 3–5). From D to E there were, in addition, transverse walls erected about every fourth or fifth pier, thus forming a series of rectangular "boxes", the bottoms of which, as soon as the pipes were laid, were concreted over. The transverse walls and the concrete bottoms were constructed at dates varying from six months to one year after the walls and piers in the corresponding position, so that pioneer communities and phases of succession were to be found in the same "box". In several cases the bottom of the "box" was at a lower level than the surrounding foreshore and consequently formed a rectangular pool developing, as will be described later, a characteristic pool vegetation. During 1936 and 1937, several of the "boxes" near D were filled with broken concrete and for a third time pioneer communities developed, this time alongside second and third year phases of the succession.

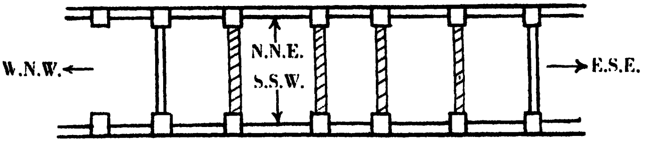


Fig. 4*a*. Plan showing arrangement and aspect of walls, piers and beams in a typical "box" near E.

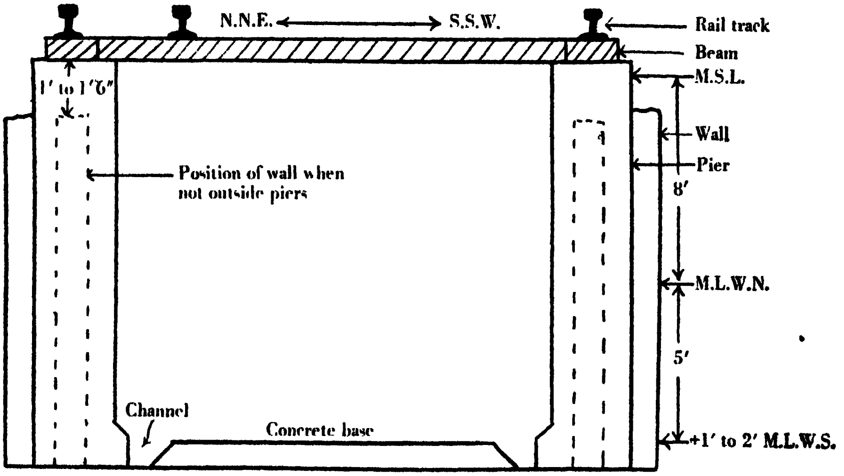


Fig. 4*b*. Diagram of section of a typical "box" near E, showing concrete base, channels, piers, walls, beams and rail-track in relation to aspect and tide level.

The main line of the construction between C and E runs E.S.E.-W.N.W. Each wall between piers had a vertical surface facing N.N.E. and S.S.W.—that is an exposed and a sheltered surface. Each pier had vertical surfaces facing E.N.E., W.N.W., N.N.E. and S.S.W., except where, towards the outfall, the wall was built outside the pier (cf. Pl. 24, phot. 5, with Pl. 23, phot. 2). Each transverse wall had an E.S.E. and a W.N.W. surface, that is, one facing the incoming tide and one protected from it. Finally, of the two parallel series of piers and walls, one was constructed on the Swansea Bay side, the other on the Mumbles Head side. The former received considerable protection from the prevailing S.W. winds and gales, the full force of which was taken by the latter. Both series received protection immediately below the middle head from C to D. There were thus set up a number of vertical and horizontal concrete surfaces varying in aspect and degree of exposure to wave action, whilst *within* each "box" the conditions were not merely more sheltered, but much more shaded, especially at the base, where surfaces were cool and damp even on the hottest days.

In comparing the succession of communities on concrete with those on wood and iron, two features were very striking: (*a*) the dominance of *Porphyra umbilicalis* in the pioneer and secondary phases and (*b*) the influence of the spread of animal communities which were absent on wood and iron. Pl. 24, phots. 5 and 6 show the piers and walls bearing copious growths of *Porphyra umbilicalis*. Several of the workmen engaged upon the construction of the outfall were fond of laverbread —which in the area around Swansea is a favourite dish for Sunday's breakfast—and week by week before leaving work on Saturday they would tear away large quantities of *Porphyra*. Yet so readily did sporelings develop on concrete surfaces that there was little apparent difference in the aspect they presented. At times the whitish concrete was almost invisible beneath a sheet of purple-brown *Porphyra* (cf. Rees, 1935*a*), and it was possible to follow the life history of this alga over a period of nearly four years (see pp. 429–31).

In presenting a summary of the observations made upon the phases of colonization, it is convenient to follow the usual primary division according to tide level.

(1) *Communities occurring from* M.L.W.S. *to* M.L.W.N.

Even during the pioneer stage there is competition at this level between algae and *Pomatoceros* and *Campanularia*. This competition is continued throughout later phases, and is in evidence in two regions in particular. Beyond the last pier a slightly raised concrete path with sloping sides was constructed in July 1935 leading to the mouth of the drain, with vertical surfaces at the extreme end about 1½ ft. (45 cm.) in depth. This path was only uncovered at spring tides. By the beginning of September small growths of *Pomatoceros triqueter* had appeared on the sloping sides and on the vertical end. At the end of the month there was a mixed growth of *P. triqueter*, *Porphyra umbilicalis*, *Enteromorpha* sp. and *Ceramium rubrum*. During late autumn and winter, *Pomatoceros* established itself as the dominant on the lower parts of each slope and on the vertical surface at the end, giving to the concrete a completely white colour, whilst on the upper parts of the slopes and the end, *Porphyra* increased in numbers and luxuriance. *Enteromorpha* was at first scanty, but towards December began, by sporelings, to dominate the horizontal upper surface of the path. The few pioneer *Ceramium* plants which survived the autumn gales were scattered amongst *Porphyra* and *Enteromorpha*. During the following spring a new invasion of *Porphyra* occurred, but on all the areas already colonized by *Pomatoceros* it was unable to germinate, and slowly through the year, *Pomatoceros* gained a fairly complete ascendancy on the sloping and vertical sides, so that at the beginning of the second year (autumn 1936) plants of *Porphyra* belonging to both spring and summer crops, were confined to the horizontal surface where in severe competition with *Enteromorpha* and later *Ulva*, it became a very minor constituent of this surface. During the second year *Ulva* and *Fucus serratus* began to appear, the latter growing quite freely on the calcareous surface of *Pomatoceros*. Before further development could take place, demolition had begun and the path covered by concrete chips, thus killing the vegetation. A comparison of the succession above described with that which took place on piers and walls on which *Balanus* spat had settled showed that whilst *Porphyra* is able to hold its own, once established, and even to replace *Enteromorpha* and other algae, there is some inhibiting factor provided by both *Pomatoceros* and *Balanus* which mitigates against the germination of *Porphyra* when in competition with either of them.

Since neither *Pomatoceros* nor *Balanus* select the spores of *Porphyra* for food, the inhibiting factor would appear to be of the nature of a toxic substance secreted by these animals during the process of building up their shell. That such may be the case is indicated, though not proved, by the following experiment. Small flat concrete chippings were fixed by "Certofix" to concrete walls during a period when *Porphyra* was sporing freely. These were removed at intervals and examined for stages in the germination of the sporelings (see pp. 429–31). After examination they were refixed to the walls. To a few of these concrete chips was added, before refixing, a few drops of a liquid in which *Balanus* spat or *Pomatoceros* (removed by careful chipping from the concrete substratum) had been shaken up. In the case of seven out of the eleven chips so treated, all save a few of the sporelings they bore were killed.

The flat concrete bottoms of the outer series of "boxes" were at about the same level as the concrete path just described, i.e. about 1–2 ft. (30–60 cm.), above M.L.W.S. Their surfaces, whilst extending the whole length of the "box", were separated from the side wall by channels, about 6–8 in. (15–20 cm.) deep, usually filled with water since the drainage hole in the wall was at the level of the main flat surface. In two of the "boxes", owing to a slight rise in shore-level outside, thus preventing drainage, the whole of the bottom formed a shallow pool. Pools and channels provided interesting contrasts in succession. Both came into existence within a few weeks of each other during July and

August, and their pioneer communities were of *Enteromorpha intestinalis*. Towards autumn *Ulva lactuca* began to appear sporadically and by the following spring was dominant on the flat bottoms of the pools, remaining dominant until the "boxes" were finally demolished. Associated with *Ulva* in the pools during the second year were a few tufts of *Ceramium rubrum*, and in the third year only was there any evidence of competition with *Pomatoceros* and *Campanularia* (and occasional *Sertularia*). By that time the number of *Ulva* plants had become so numerous as to form an almost complete carpet, leaving little room for the calcareous shells or creeping stolons to develop. Although the thalli of *Ulva* die back in winter, their attachment organs are perennial, and dense masses of sporelings fill up any available spaces from May to September. A few sporeling *Fucus serratus* appeared in the third year, growing on the *Ulva* thalli, but demolition took place before further observations could be made.

In contrast to this sequence in the pools, leading to the dominance of *Ulva*, the succession in the channels led to animal communities dominated by *Pomatoceros triqueter* and *Campanularia flexuosa*. Before the first autumn invasion of *Ulva*, the sides of the channels began to show small local patches of these two species, so that whereas in the pools the former quickly gained dominance in the first year, it had to compete in the channels with the two animal species. Although quite abundant at first, its spores failed to increase materially the area colonized, and in the second year was no more abundant than *Ceramium rubrum* which had invaded the channels during the summer (9–10 months after construction). During the months which preceded the final demolition, the community in the channels consisted of:

Pomatoceros triqueter	30%	Chondrus crispus	8%
Campanularia flexuosa	40%	Enteromorpha sp.	
Ulva lactuca	10%	Ectocarpus sp.—a few tufts	
Ceramium rubrum	10%	Balanus balanoides—a few stray individuals	

[In parts *Sertularia* (*Dyanema*) *pumila* occurred together with *Campanularia*.]

Both the channels and pools were under practically identical ecological conditions (tide level, submergence, nature of substratum, etc.), but there were three differentiating factors (*a*) temperature, (*b*) light and (*c*) angle of slope. Owing to their proximity to the walls, the channels were more shaded from direct sunlight than the more open concrete bases of the pools. During summer and autumn the water in the pools was, after 2–3 hr. exposure to direct sunlight, 5–6° C. warmer than that in the channels. This slight increase in temperature certainly appeared to affect the degree of spore production in *Ulva*, for during equivalent fruiting periods, the thalli in the pools bore a much higher percentage of pale or colourless fringes (indicating empty sporangia) than did those in the channels. Not only was a much larger number of spores produced, but on coming to rest in the pools they appear to have germinated more readily and rapidly under the slightly warmer conditions, and thus colonized bare patches with greater success than in the cooler channels. In view of the interpolation of a medusoid phase in the life history of *Campanularia*, the temperature factor is probably of less account, but both *Pomatoceros* and *Campanularia* favour situations (e.g. on or under pebbles, stones, overhanging ledges) which are definitely more shaded and cooler than exposed rock surfaces at the same tide level. Consequently the channels provided better habitats, and with freedom from severe competition with *Ulva*, they gained an ultimate ascendancy.

As in other situations, the third factor—angle of slope—is of considerable importance in the channels, especially as it affects *Pomatoceros*. The sides are at about 60°, sufficiently steep to be of importance as a factor mitigating against the ready settlement of algal spores, and favouring the growth of *Pomatoceros*. From a consideration of all the situations in which this worm grows on the coasts of Gower, it is evident that, whilst it will grow quite well on flat surfaces or slight slopes, it succeeds best on those which are vertical or steeply sloping. Further, algal spores do not appear to be able to grow on its chalky tube and once established it tends to extend at the expense of other organisms (see Fisher-Piette, 1932).

The communities of the pools and channels above described lie within the "boxes" at roughly 2 ft. above M.L.W.S. At similar levels immediately outside, the base of the walls and piers was practically bare owing to trituration by sand and other particles lying on the foreshore in the vicinity. Between M.L.W.S. and M.L.W.N. there is a difference of about 7½ ft. (*c.* 2·3 m.) whilst the vertical distance between M.L.W.N. and the top of the piers is about 7¾ ft. (2·35 m.). Only near E did the vertical range of concrete surface approach these combined figures when piers 13½ ft. in height were erected. In the main the height of the walls inside the "boxes" was 7–10 ft. (2·13–3·04 m.), and that of the piers 10–12 ft. (3·04–3·66 m.). Measurements outside varied from 2½ to 12 ft. (0·75–3·66 m.) owing to great variations in the shore level or local accumulations of sand. The communities of the piers and walls fall into two chief groups, (1) those growing at about M.L.W.N., but spreading a foot or two above or below this level and (2) those which were wholly above M.L.W.N. and approximated to M.S.L.

(2) *Communities occurring near* M.L.W.N.

At no time could it be said that there was any fixed distribution of communities at this level, great variation existing from "box" to "box". The following is a summary, for instance, of the conditions prevailing during a visit in March 1937.

Box 1 (*nearest to E*). (*a*) W.N.W. and E.S.E. walls barren except for *Enteromorpha compressa* and *E. intestinalis* at about 4½ ft. (1·37 m.) above M.L.W.N.

(*b*) N.N.E. and S.S.W. walls had scattered *Porphyra* from about 4 ft. (1·22 m.) below M.L.W.N. to 4½ ft. (1·37 m.) above.

Box 2. All walls had topmost 2–3 ft. (0·6–0·9 m.) colonized by *Enteromorpha* spp. with *Pomatoceros* at the base, and *Ulva* on some of the pillars. No *Porphyra* at all.

Box 3. (*a*) All walls save N.N.E. had *Porphyra* scattered from base to apex. Several *Patella*, and occasional plants of *Ceramium rubrum* and *Chondrus crispus*. No *Enteromorpha*.

(*b*) N.N.E. wall had copious growths of *Ulva* and luxuriant *E. compressa* and *Porphyra*, the latter two mainly above M.L.W.N.

Boxes 4 *and* 5. Both had walls practically black with *Porphyra* thalli adhering to them. No *Balanus*, no *Ulva*, and only a little *Enteromorpha* near the top.

Box 6 (*midway between E and D*). (*a*) W.N.W. wall. Abundant *E. compressa* near M.S.L.: mixed community of *E. compressa* and *Porphyra* towards M.L.W.N.: scattered *Pomatoceros* on plinths at bottom.

(*b*) E.S.E. wall. Very little *Enteromorpha compressa* near M.S.L. and none lower down, but abundant *Porphyra* from base to apex. A few scattered *Balanus*.

(*c*) N.N.E. wall. Luxuriant growths of *Enteromorpha* spp. and *Porphyra* near the top, with almost pure band of *Ulva* about 3 ft. (0·9 m.) in depth about 2–5 ft. (0·6–1·52 m.) above M.L.W.N. Scattered *Patella* and several local clumps of *Mytilus*. Numerous *Littorina littoralis*.

(*d*) S.S.W. wall. Comparatively little *Enteromorpha* or *Porphyra*. *Balanus* very abundant, with a few *Patella* and a few scattered *Mytilus*. *Pomatoceros* at the base, especially on the plinths.

Boxes 7–9. These showed considerable invasion by fucoids, which were dominant over all other communities.

Much of the divergence between the communities present on the walls of a single box, as well as between those of adjacent ones, is due to difference in the date of erection, walls facing E.S.E. and W.N.W. having been built from 6 to 18 months later than those facing N.N.E. and S.S.W. Between the time of arrival of the pioneer communities and the appearance of *Fucus* sporelings at the end of the second or beginning of the third year, the community or communities present depend upon an intimate interaction of biological and ecological factors.

(1) *Pioneer community of* Porphyra umbilicalis *f.* linearis *in winter*. The thalli frequently lie so closely together in sheets that there is little room for spores of other algae to develop in spring. Thus the ubiquitous *Ulothrix-Urospora* phase is scarcely represented. During spring and summer, spores from f. *linearis* will extend the area colonized by *Porphyra*, for as plants of the *Ulothrix-Urospora* phase dry up and die on other parts of the walls their place is taken by the new crop of *Porphyra*. Only on walls facing S.S.W. and exposed to strong insolation and drying, are many plants killed at the height of summer. If the amount of *Porphyra* becomes, in this way, extensive, there is no serious

competition from *Ulva*, *Enteromorpha compressa* or *Balanus*, so that for a year at least the box will be almost exclusively populated by *Porphyra*, e.g. nos. 4 and 5 (see p. 426). During the second year the above sequence may be repeated, but usually two factors influence the succession.

(*a*) A period of bad weather or heavy pollution may coincide with a reproductive phase of *Porphyra* less vigorous than usual. Other algae then have a greater opportunity and a mixed community will develop. It may happen—as on the N.N.E. wall of box 3—that temporary favourable conditions may coincide with the fruiting period of one of competing algae—in this case *Ulva*—and an ascendancy thus attained.

(*b*) Some local conditions leading to an increase of dampness will favour *Ulva* at the expense of others: thus, e.g. in box 3, owing to the temporary dumping of certain materials at its base, there was more churning of the water and more spray cast, resulting in damper walls upon which *Ulva* succeeded, whereas on drier parts it failed.

(2) *Pioneer community of* Ulothrix *and* Urospora *in spring.* The amount of this community reaching to levels as low as M.L.W.N. is very little and considerable patches of bare rock were available both for *Balanus* and later algal colonizers. Only in two years, 1935 and 1937, did *Balanus* spat arrive in sufficient quantity to be an important competitor. The surface upon which it settled was not invaded by any algae until the Fucaceae appeared. It would therefore appear that, as in the case of *Porphyra* (see p. 423), a toxic substance may be produced preventing the germination of other algal spores. Competition was therefore confined mainly to *Porphyra*, *Enteromorpha compressa* and *Ulva*, all of which spore freely from May to August. When spores of all three arrived, *Porphyra* and *Enteromorpha compressa* survived better on the more exposed E.S.E. and S.S.W. walls, *Ulva* drying off during hot spells, but on the more shaded N.N.E. and W.N.W. walls it survived, and by proliferation and sporelings during the second year not only kept its place but increased greatly the area it had colonized the first year. Local differences in density between *Porphyra* and *Enteromorpha* appeared to be due purely to the chance arrival of denser aggregates of spores on bare regions of the wall.

It frequently happened that long periods of rough weather would clear the walls during autumn; and the bared surfaces would be colonized by *Porphyra umbilicalis* f. *linearis* in winter or *Ulothrix-Urospora* in spring. Only when the Fucaceae became established was there any real permanence in the vegetation. During the second year numerous, but scattered, plants of *Ceramium rubrum* appeared nearer the base of the walls and piers, but neither these, nor stray individuals of *Patella* or *Littorina*, nor local small clumps of *Mytilus*, affected the succession.

(3) *Pioneer communities of* Porphyra, Enteromorpha *and* Campanularia *in summer. Campanularia* was confined to very damp surfaces and ledges of the plinths, and once established it tended to spread and keep out all algae in later

phases. With so large a surface to colonize, competition between *Enteromorpha compressa*, *E. intestinalis* and *Porphyra* did not assume important proportions during the pioneer stage. In autumn both spp. of *Enteromorpha* died off at such low levels, leaving *Porphyra* (continuing through the winter phase as f. *linearis*) to establish itself as a definite dominant in the spring of the following year. As tides recede they leave the thalli of *Porphyra* adhering closely to the concrete. At the same time they deposit at their edge spores of other algae, so that if the *Porphyra* thalli are growing at all thickly, spaces between them are few (see Pl. 24, phot. 6) and invading algae are kept in check. Factors already described in (i) and (ii) above, however, tend to keep the community an open and changing one even in the third year, unless there is an invasion by Fucaceae. The oospores of the latter find a suitable settling place and conditions favourable to germination amongst the crowded thalli of *Enteromorpha*, *Porphyra* and *Ulva* (see also p. 434).

(4) *Pioneer communities of* Enteromorpha compressa *and* Porphyra *in autumn.* In most cases plants of *Enteromorpha compressa* which developed as late as the autumn did not, at M.L.W.N., survive the winter, so that only *Porphyra* remained on till spring. Succession then followed as set out in (i).

Summing up the succession on concrete in the region of M.L.W.N.:

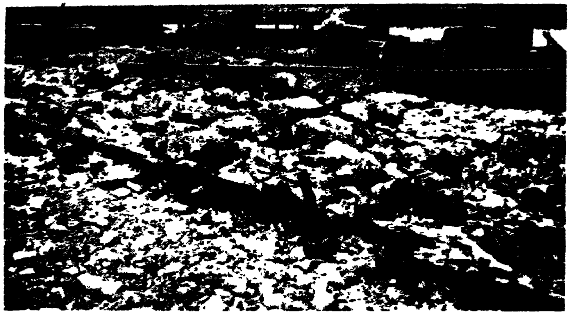
(1) The animals concerned were *Patella*, *Mytilus*, *Balanus*, *Littorina*, *Pomatoceros* and *Campanularia*. Of these only *Balanus* and *Campanularia* played any significant part, the others being too widely scattered to be of importance.

(2) The algae concerned were *Enteromorpha compressa*, *E. intestinalis* (rare), *Porphyra umbilicalis*, *Ulva lactuca*, together with occasional scattered individuals of *Ceramium rubrum* and *Chondrus crispus*. Season, frequency and abundance of spore production, amount of shade and dampness, the habit of the species and probably certain toxic effects, determine the presence and relative abundance of the first four.

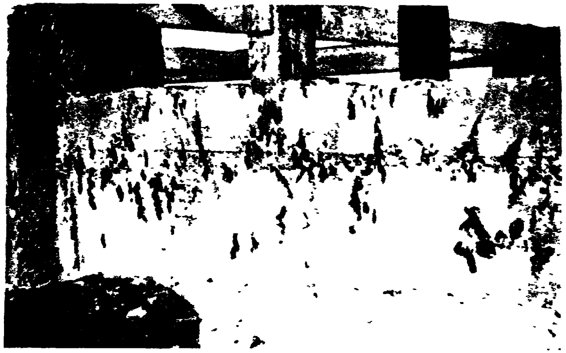
(3) *Fucus vesiculosus* and *F. serratus* did not appear until at least 20 months (more usually 2½–3 years) after the pioneer community.

(3) *Communities occurring about* M.S.L.

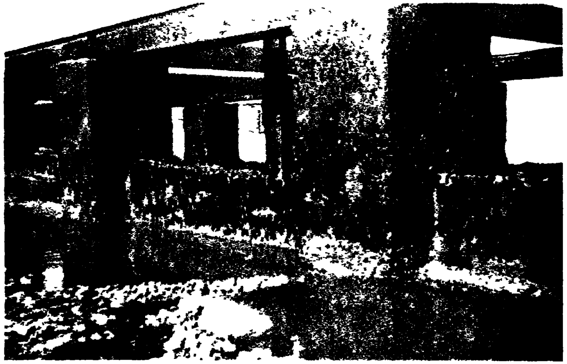
Those parts of piers and walls occurring within 1–2 ft. (0·3–0·6 m.) of M.S.L. were colonized almost exclusively by *Enteromorpha compressa* var. *nana* and *E. compressa* showing a very distinct zonation, the finely branched thalli of the former occurring as an almost felt-like growth above the latter, especially upon the horizontal surfaces at the top of the walls. Except for local interruptions by *Porphyra*, these two algae continued to dominate this region until the invasion of *Fucus vesiculosus*, beneath the thalli of which they continued for a while, but eventually during the third year they disappeared almost entirely. The occurrence of *Porphyra* was due to the erection of piers or walls at a period coincident with very active spore production on the part of this



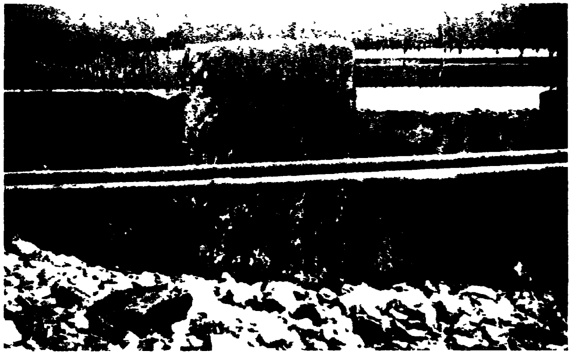
Phot. 3. Region near C. All dark patches on beams, piers, walls, pipes and limestone blocks represent growths of *Porphyra*.



Phot. 4. Recently erected walls and piers (S.S.W. aspect), showing early stage of colonization by *Porphyra*.



Phot. 5. Wall erected two months earlier than that in 4, showing rapid colonization by *Porphyra*. S.S.W. aspect.



Phot. 6. Rails, beams, piers and walls with *Porphyra*, but none on iron pipes.

alga, which became the pioneer and by its adhering thalli and almost continuous production of spores (see p. 430) maintained its dominance until the coming of *F. vesiculosus*. On walls where both *Porphyra* and *Enteromorpha* occurred as pioneers, conditions at this level appeared to favour the latter, for *Porphyra* soon disappeared and in its place developed new sporelings of *Enteromorpha*.

Several of the piers and walls at this level were either entirely or almost completely barren for most of the period until the arrival of *Fucus*. The cause of this barrenness was obscure, since walls and piers at similar levels and erected at about the same time were clothed with *Enteromorpha*. It is just possible that local currents, due to structural features, led to eddies and the longer retention of polluted water, the oil from which, clinging to the tops of the walls, prevented spores from germinating.

Finally the communities at both M.L.W.N. and at M.S.L. were more luxuriant whenever shelter was afforded, as for instance in the region from C to D, where the colonization was far more dense and the individual plants, notably of *Fucus vesiculosus* and *F. serratus*, were much larger than those of corresponding ages from D to E.

10. ECOLOGY AND BIOLOGY OF *PORPHYRA UMBILICALIS*

By far the most striking feature of the investigation was the abundance of *Porphyra*, more especially on the concrete, but at times also on iron and wood. It was possible to observe closely its life history, a full account of which will be published separately, and to note certain features of its biology and ecology about which differing opinion has been expressed in the past. The genus has been investigated by several authors in recent years (Kylin, 1922; Grubb, 1924; Dangeard, 1927, 1931), and there appears to be general agreement that plants bearing neutral spores (monospores, gonidia) are rare (Grubb and Kylin failed to find them) and that carposporic plants are abundant and may be found fruiting at almost any time of the year. On the south coast of England and at Quiberon Dangeard, 1927, p. 211) the plants disappear almost completely with the onset of more intense insolation in spring and early summer. At Mumbles Head a *Porphyra* community is to be found throughout the year, but the life of an individual plant rarely exceeds 8 months. It will be convenient to begin with the production of carpospores by the f. *linearis*. The earliest date at which carpospores were found on these narrow thalli was 10 December; they were frequent in late December and were abundantly produced from January to early March. By means of observations on concrete chippings (see p. 423) it seems fairly certain that the carpospores do not germinate into new *Porphyra* plants, but that they produce short sparingly branched filaments from which non-motile spores are liberated. Amongst several dozen plantlets which were removed from the chippings the great majority were branched and the terminal cell, or in some cases the penultimate cell, was empty. In seven cases examined, four or more cells were empty. It is therefore clear that spores are liberated. These plantlets, whose life is about 4 weeks, may be compared to the plethysmothalli of Sauvageau (1927). In no case was there any evidence of thalli developing from these filaments—that is to say they do not appear to be of a protonematal character.

The f. *linearis* later develops into the *umbilicalis* type. From about the end of February the long narrow thalli begin to widen and become wavy at the margin, and by April would be identified as *Porphyra umbilicalis*. Side by side with plants undergoing such changes there occur small plants which develop directly into the umbilicate type. Since the carpospores from f. *linearis* appear always to develop into minute filamentous plantlets, this new generation can only have arisen from (*a*) dormant or resting spores from the previous year or (*b*) spores from the plethysmothalli, derived from the carpospores. There is no evidence either from cultures (Grubb, Kylin, Yendo) or from the concrete chippings that any resting spores are produced, so that it seems legitimate to suppose that spores from the plethysmothalli germinate directly into umbilicate plants.

Both kinds of umbilicate plants (i.e. those derived by a modification of f. *linearis* and those developing from spores) continue to produce carpogonia and spermatia, and eventually carpospores until late July, and chippings examined showed plethysmothalli up to mid-August. Although insolation is strong at Mumbles Head, *Porphyra* does not disappear and rocks, concrete, iron and wood are plentifully covered throughout the summer months. Such plants are almost entirely the new spring umbilicate crop, for those derived from f. *linearis* begin to decay in May and soon disappear completely.

During August, gonidia are formed and continue to be produced until about mid-October, after which most of the spring crop of plants die back. These gonidia show signs of rapid germination and within a few weeks develop into f. *linearis*, continuing to elongate slowly until about 10–12 cm. in length and rarely exceeding 1–1½ cm. in width. When about 5 cm. in length they show signs of carpogonia and by mid-December carpospores are beginning to be shed. The life history of *Porphyra umbilicalis* at Mumbles Head may be summarized as follows:

I. *August–November:* gonidia germinate to produce f. *linearis*.

September–February: f. *linearis* dominant but mixed with *Porphyra umbilicalis* type B.

December–February: f. *linearis* produces carpospores.

February–April: f. *linearis* gradually changes into *Porphyra umbilicalis* type A.

April–July: type A produces carpospores.

May–August: type A begins to decay and finally to disappear.

II. *December–February:* carpospores from f. *linearis* germinate into plethysmothalli.

April–July: carpospores from type A germinate to produce plethysmothalli.

January–August: spores released from plethysmothalli (of whatever origin) produce new crops of type B.

March–August: type B produces carpospores which give rise to a further crop of plethysmothalli.

August–November: type B produces gonidia (I have no evidence of gonidia being produced on type A).

November–February: type B, having produced gonidia show signs of decay and most of the plants have disappeared by February.

A consideration of the above summary shows that some form of reproductive activity is taking place throughout the year. Germinating spores have to compete mainly with *Enteromorpha* spp., *Ulva*, *Fucus vesiculosus*, *Balanus balanoides* and *Pomatoceros triqueter*. In competition with other algae, the decisive factor in spring and summer appears to be numerical superiority: in this the rapid augmentation brought about by the plethysmothalli is important. Except near M.S.L. where competition with *Enteromorpha compressa* and *E. intestinalis* is severe in late summer, and in pools or damp shady places, where competition with *Ulva lactuca* may be found, the immense number of spores produced by *Porphyra*, whilst in the pioneer phase, enables it to compete successfully with other algae in later stages of the succession. In autumn and winter it has the field largely to itself, for only *Enteromorpha compressa* amongst its competitors is fruiting to any considerable degree. The patchiness of its distribution within some of the "boxes" is due largely to surf action tearing away spores or sporelings during periods of low productivity on its part, and its absence from the outside walls, especially those facing S.S.W., is due to both exposure to surf action and to more intense insolation. In competition with *Balanus*, it should be noted that, at the time that spat is settling (March–April), *Porphyra* will be in one of three states: (*a*) f. *linearis* will be changing into the umbilicate form: this is unaffected by the spat; (*b*) plethysmothalli will be developing: these may be poisoned if the quantity of spat is very great (i.e. if they settle side by side in dense sheets); (*c*) young plants of the umbilicate type B will be growing and may be either poisoned or smothered by dense settling of spat. If individuals of *Balanus* are separated by distances of 1 cm. or more, or if the spat settles in small local colonies separated by wide spaces, *Porphyra* may form a joint community—as on the S.S.W. wall of "box 6" (see p. 426). In the main, however, the spring competition between the two leads most often to a triumph of *Balanus* on uncolonized surfaces, but on surfaces already in occupation by *Porphyra*, whose thalli cling fast to the surface, *Balanus* has little chance to settle.

With regard to *Pomatoceros triqueter*, competition appears to take place mainly in the autumn when the gonidia of *Porphyra* are developing into f. *linearis*. In the very localized areas where *Pomatoceros* has already established itself, it prevents the invasion of *Porphyra* by (*a*) its rate of spreading over the surface, (*b*) its toxic effect (see p. 423) and (*c*) the inability of gonidia to germinate on the calcareous tube.

11. THE RESTRICTION OF THE ALGAL COLONIZERS

The algal flora of the Mumbles Head region consists of 9 Myxophyceae, 13 Chlorophyceae, 22 Phaeophyceae and 41 Rhodophyceae. Of these only 2 Myxophyceae, 8 Chlorophyceae, 6 Phaeophyceae and 6 Rhodophyceae took part in the colonization. It may be presumed that spores of most, if not all, of the species growing in the vicinity of Mumbles Head would be brought, during the 4½ years, into contact with the very extensive total surface of concrete, wood and iron exposed. That so large a number of such species did not, in fact, take part in colonization may be explained by the following considerations:

(*a*) Certain species are obligate epiphytes whose hosts were absent from the new surfaces, e.g. *Myriactis stellutata*, *Polysiphonia fastigiata*.

(*b*) Certain species are mainly psammophilous (*Polyides rotundus*), limicolous (*Microcoleus chthonoplastes*) or occur in deep pools (many Rhodophyceae).

(*c*) Certain species have a bathymetric range outside that provided by the new surfaces (*Laminaria* spp., many Rhodophyceae, *Rivularia nitida*).

When allowance has been made for such species, there remain about 30–35 which might be expected to colonize the concrete, iron and wood. In view of the fact that the Fucaceae did not appear usually until the third year, it may well be that certain other species might have invaded the area had the time available been longer. Nevertheless, it has been very surprising to find that certain very common species, growing plentifully on rocks or boulders in the vicinity, and within the requisite tide levels, did not find a place on surfaces where competition was not severe and even, at places, absent. Observations made during the investigation do not warrant any definite pronouncement as to the factors which mitigated against these algae acting as colonizers, but the following tentative suggestions are put forward in partial explanation in certain cases.

(i) *Cladophora rupestris*. As had been pointed out previously (Rees, 1935*b*) this alga flourishes best where there is an admixture of fresh water. The absence of any source of fresh water, of which this alga—along with *Enteromorpha intestinalis*—is an indicator along the coast of Gower, may explain its absence.

(ii) *Cladophora sericea*. Lack of a sufficient protective covering of larger algae, particularly Fucaceae.

(iii) *Leathesia difformis*. In Gower it is usually epiphytic on *Corallina*, *Laurencia* and other algae, which are absent from the construction. Absence of suitable hosts for adelophycean stage.

(iv) *Cladostephus spongiosus*. This alga appears to grow best on sand-covered rocks (sand fixed by *Rhodochorton*), and the absence of a suitable habitat may account for its non-appearance.

(v) *Ascophyllum nodosum.* Absence of good anchorage on vertical surfaces (cf. Cotton, 1912; Rees, 1931).

(vi) Both *Pelvetia canaliculata* and *Fucus spiralis* are very rare, partly because the only situations within the appropriate tide levels were the stages at B, C and D, and the travelling crane. Vertical wood surfaces until much roughened by wave action and weathering are unsuitable for lodgment of the large oospores of these two algae (see also p. 416).

(vii) *Laurencia pinnatifida.* It is difficult to understand the absence of this alga, which is very abundant on nearby rocks and does not appear to be affected by angle of slope. Young plantlets were developing in the vicinity from M.S.L. to M.L.W.S. throughout the period of investigation.

(viii) *Lomentaria articulata.* The plinths and shaded bases of the piers seem to afford a suitable habitat for this alga—but the absence of large overhanging algae may account for its absence.

(ix) *Dumontia incrassata.* This alga shows seasonal migration and the pools at the base of the "boxes" would have afforded a suitable habitat for the spring and summer plants. In this case, as possibly with various fairly common species of *Polysiphonia*, *Ceramium* and *Callithamnion*, free access to the inside walls was difficult because of their height, whilst colonization of the vertical walls on the outside was prevented because of trituration or more intense exposure to the sun. In this connexion it is important to notice that the spores of many marine algae sink after liberation, and if fruiting coincides with periods of calm weather, such spores will not be carried over the top of the wall, but if carried at all will tend to drift inshore at the edge of the tide. The fact that such common species as *Pylaiella littoralis*, *Ceramium rubrum* and *Chondrus crispus* are only occasionally found on the new surfaces indicates that the chances of spores being carried to, and deposited on, them is rather meagre in a period so short as four years.

(x) *Corallina officinalis.* The presence of a small amount of mud and of decaying material favours the growth of this species: the walls and bases were too well scoured to allow any such material to accumulate.

Finally, in regard to all the above fairly common algae as well as those occurring less frequently in the neighbourhood, there would be the effect of a temporary accumulation of polluted water (see p. 407) within the "boxes", and especially between A and C. It has been shown that spores of freshwater-algae (see Fritsch, 1931) are sensitive to very slight changes in pH value.

12. THE ULTIMATE DOMINANCE OF THE FUCACEAE

Pelvetia canaliculata liberates its oospores from May to September, *Fucus spiralis* from March to November, *F. vesiculosus* mainly in June and July, but like *F. serratus* (maximum in autumn and winter) receptacles may be found all through the year. There is therefore no part of the year during which reproductive activity amongst the Fucaceae is at a complete standstill, yet fully 90% of the plants of this group do not establish themselves until late in the second year or during the third year after the surfaces have become available. It would appear, therefore, as if some preparation was necessary before the Fucaceae could establish themselves. Their oospores, especially those of *Pelvetia* and *Ascophyllum*, are much larger than the spores, gametes and gonidia of the pioneer algae, and it seems highly probable that in a nidus provided by the living or decaying thalli of such algae as *Porphyra umbilicalis, Enteromorpha intestinalis, E. compressa, Ulva lactuca*, or amongst the sheets of *Ulothrix, Urospora* and *Bangia*, these large oospores would be able to settle between tides and, protected from wave action and kept moist by contact with such thalli or filaments, would be able to remain sufficiently long to germinate. Protection would be afforded also to the first rhizoidal filament put out for anchorage. Once established, the growth of their holdfasts, and the shade cast by their developing thalli, would enable them to compete successfully with algae which preceded them, and as these, being short-lived, died the dominance of the Fucaceae would be assured. Their closely overlying thalli would prevent spores, carried by the tide, alighting on the wood or concrete surface, so that no new subvegetation would develop. [On rocks in the vicinity subvegetation in the bands of *Fucus vesiculosus, Ascophyllum* and *Fucus serratus* is absent beneath aggregates of young thalli, but as the stipe thickens and becomes more rigid, lifting the basal end of the thallus, spores are able to get to the rock surface and species of *Cladophora, Ceramium, Polysiphonia, Gelidum, Laurencia* begin to form a subvegetation two or three years after the germination of the fucoids.]

It does not, of course, follow that preparation of the kind referred to above is always necessary before colonization by Fucaceae. Normally, on rocky shores, there is already plenty of vegetation, including parent plants, to give protection and stability to the germinating oospores. But on the predominantly vertical sides of concrete and wood investigated, lodgment of oospores on the bare surfaces exposed to wave action would be very rare, and as has been mentioned above, not more than 10% of the fucoids present succeeded in germinating until the habitat had been suitably prepared.

13. BIOTIC REACTIONS

It is difficult to carry out an ecological investigation of the littoral region without being impressed by the intimate interrelationships of the plants and animals of which it is composed. Little attention appears to have been given to the precise nature of the phenomena involved. Most papers dealing with the ecology of marine algae make but a passing reference to animals or animal communities, whilst in publications dealing with the littoral fauna, algae are considered mainly from the point of view of the food, protection or substratum which they afford. [Note, however, Kitching (1937), Fischer-Piette (1932).]

Whilst the presence or absence of certain communities of marine algae, such as the belts of the Fucaceae, the zones of *Laminaria*, *Gigartina*, *Laurencia*, *Rhodymenia*, *Corallina* or encrusting Rhodophyceae can be related to well-defined ecological factors such as degree of exposure to wave action, period of submergence, aeration of water, changes in salinity, light, etc., there are other communities of saxicolous algae whose distribution is so sporadic and whose occurrence so spasmodic that explanations regarding them must be sought in factors concerned with their life history or their competitive relationships with other littoral algae or animals. This is certainly the case with those algae which have an adelophycean stage in their life history. The minute plantlets of this phase have to find a suitable nidus in which to spend their active period, and if a large percentage of them fail or if they suffer serious damage, the reappearance of the delophycean stage will be seriously affected. The nature of the struggle between *Porphyra umbilicalis* and *Balanus balanoides* illustrates what may happen locally when the competing species are numerically fairly well balanced over a wide area. When any disproportion occurs, either in the numbers of parent plants or in the numbers of spores produced, the very intense normal competition between the vast numbers of spores, eggs and other reproductive units produced by littoral flora and fauna accentuates the disadvantage under which the numerically inferior species competes. Another side of this picture is presented by the preparation by pioneer species, or those occurring early in the succession, of suitable habitats for those entering later as e.g. *Enteromorpha* spp., *Porphyra*, *Ulva*, *Ulothrix* spp., which provide possible resting places for fucoid oospores. On land the pioneer plants and animals influence the soil, which in turn conditions the plants and animals of the next phase, and the cycle continues until a relatively stable, yet dynamic climax is reached. Except in pools, shallow bays, mud flats and salt-marshes, the soil factor or its equivalent (chemical constitution, concentration, *p*H) is absent from the littoral region, and the continuity of the climax dominants (Fucaceae, *Laminaria* spp., *Laurencia*, *Gigartina*, *Balanus*, *Mytilus*, etc.) is quickly attained and thenceforth maintained by proliferation or vast egg or spore production, invaders being kept away by closely packed or overlying thalli (see also p. 434), or possibly by toxic effects, as suggested by Zaneveld (1937) for the well-defined limits of zones of Fucaceae in the upper part of the littoral region. Under such circumstances it is evident that biennials, pseudo-perennials, and perennials will have a great advantage, for at no period are they absent (except for well-defined ecological reasons) from the rock surface and that—as this investigation has shown—it is only during a very brief period (2–3 years) following the exposure of new surfaces that more transient species come into prominence.

14. SUMMARY AND CONCLUSION

1. For periods varying from 9 months to 4½ years, new surfaces of iron, wood and concrete were constructed at Mumbles Head, near Swansea, and were colonized by marine algae and animals.

2. Partly because of geological and hydrographical conditions, and partly because of features relating to the biology of species in the vicinity, the number of algae and animals taking part in the colonization was very limited.

3. The greater part of the colonization took place between M.S.L. and M.L.W.S., but across the inner sound and on stages and cranes, surfaces were exposed from M.H.W.S. to M.S.L.

4. Pioneer communities chiefly of *Porphyra*, *Enteromorpha* spp., *Ulothrix*, *Urospora* and *Balanus*, depended upon the season of the year and upon the reproductive activity of particular species.

5. Later phases on iron were patchy and discontinuous; on wood they were limited by the restricted tide level, but served to emphasize the general trend on concrete.

6. Concrete surfaces bore a varied flora and fauna, depending upon aspect, exposure to wave action, light, temperature, tide level and also upon the biology of the species concerned.

7. The phases of succession leading to the ultimate dominance of certain Fucaceae are considered in detail.

8. New facts relating to the life history of *Porphyra umbilicalis* are given, notably the existence of an adelophycean phase.

9. Attention is drawn to the importance of considering the littoral region as a Biome.

The occurrence and distribution of communities of marine algae within the littoral region have been the subject of several investigations in recent years (Colman, 1932–3; Gibb, 1939; Grubb, 1936; Kitching, 1937; Knight & Parke, 1931; Rees, 1935*b*; Zaneveld, 1937) and it appears that there is, within any restricted area such as a sheltered bay or an exposed coast, a stability and a continuity of the chief communities in spite of the very short life of the dominants of which they are composed. Naturally occurring new surfaces are very rare, depending upon cliff-fall or tidal shift of sand exposing rocks hitherto buried, and seral stages do not appear to have been studied in any detail. The present investigation has thrown light upon some of the factors concerned in the progress towards a *Fucus*-dominated climax, notably the effect of temperature, aspect, slope, tide level and substratum upon the competition between the reproductive bodies of both algae and animals which come to rest upon new surfaces of iron, wood and concrete. It has also shown that pioneer communities may actually prepare the way for later phases of the succession and has emphasized the importance of biotic reactions.

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THE INFLUENCE OF RABBITS ON THE VEGETATION OF CERTAIN HILL-GRAZING DISTRICTS OF SCOTLAND

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The terrain of the present study lies in the same districts of the Moorfoot and Pentland Hills as the "Screes" considered in a previous publication (Fenton, 1939).

All the hill areas are grazings almost without exception, except a few places where trees may be found as at Glen Tress, near Peebles. The elevations of the parts considered vary from about 500 to 1200 ft. above sea level. The rock and soil formation are similar to those previously considered (Fenton, 1939). In every case the rabbit burrows are in sand, sandy or light soil, often with small stones or rubble lying not far beneath the surface. There is frequently a thin covering of peat overlying the soil and stones. No burrows have so far been found in deep peat, heavy or wet soil.

As sheep have been the chief grazing animals over these hills for a very long time, the natural vegetation has been considerably changed (Fenton, 1937) before rabbits still further modified local vegetation. Hence, rabbits within recent years, by their extraordinary increase in numbers, are changing the vegetation near their burrows after it had reached a biotic climax due to sheep. Whether this further local interference by rabbits should be regarded as a deflected succession will not be considered at present. It is necessary, however, to point out that the introduction of cattle to hill grazings previously pastured by sheep can change Nardetum to an *Agrostis-Festuca* association (Fenton, 1937). No two animals have the same effect on vegetation which is grazed, hence the importance of the rabbit and its menacing increase.

So far rabbits are living in isolated communities, but unless the present rate of increase is checked, continuous areas may be affected where sheep will no longer be the dominating influence. It is well, therefore, to investigate the present conditions so as to estimate the changes likely to occur. The following examples are selected as typical of the vegetation found around burrows where rabbits are plentiful. In almost every case the burrows are facing the sun, for it is comparatively rare to find a burrow of any size on the shaded northern slope of a hill. In this study *Agrostis palustris* Huds., *A. canina* and *Festuca ovina* agg. (including *F. rubra*) will be grouped under *Agrostis-Festuca*, a frequent and well-known grassland association (Fenton, 1934).

No. 1. PENTLAND HILLS

The vegetation is now: *Deschampsia flexuosa* (d.), *Galium saxatile* (s.d.), *Vaccinium Myrtillus*, *Nardus stricta*, *Agrostis-Festuca*, *Poa annua*, *Luzula campestris*, *Hylocomium cupressiforme*, *Hypnum Schreberi*, and *Hylocomium squarrosum*. Originally the vegetation was a mixture of *Vaccinium Myrtillus*, *Nardus stricta* and *Agrostis-Festuca*. *Vaccinium Myrtillus* and *Nardus stricta* are giving way before grazing pressure, *Deschampsia flexuosa* is also heavily grazed.

No. 2. PENTLAND HILLS

Deschampsia flexuosa dominant but very closely grazed, *Galium saxatile* (s.d.) is not grazed. *Agrostis-Festuca* is generally grazed and *Deschampsia caespitosa* is disintegrating after very close grazing. This vegetation was derived from a typical *Agrostis-Festuca* grassland.

No. 3. PENTLAND HILLS

Galium saxatile (d.) shows no signs of grazing. *Urtica dioica* is slightly grazed; this is rather exceptional. *Digitalis purpurea* is grazed and also *Holcus mollis* (rather unusual). *Agrostis-Festuca* is closely grazed, but *Veronica Chamaedrys* is only slightly grazed. Clumps of *Ulex europaeus* are closely grazed with *Agrostis* spp., *Festuca ovina* and *Galium saxatile* growing through the bushes, and in that position ungrazed. This area was originally on rather dry *Agrostis-Festuca* association with clumps of *Ulex europaeus*.

No. 4. PENTLAND HILLS

This is an example of extreme rabbit pressure. There are isolated patches of *Agrostis* spp., *Festuca ovina* and *Deschampsia flexuosa*, all of these severely grazed. *Galium saxatile* is widespread and dominant. *Ulothrix* spp. is present on much of the bare ground. The rest is loosely covered by *Cladonia pyxidata*, *C. rangifera* and *C. coccifera*, as well as some *Peltigera canina* and *Lophocolea bidentata*. The original vegetation was an *Agrostis-Festuca* grassland.

No. 5. PENTLAND HILLS

This area was a young wood plantation bordering agricultural land and on the other side rough grazings. Young trees of Scots pine and spruce were heavily damaged, the damage varying from 45–70% of deaths. *Ulex europaeus* and *Digitalis purpurea* are both severely grazed. *Holcus mollis* is slightly grazed, but *Galium saxatile* is untouched, spreading and gradually assuming a dominant position in places. *Mercurialis perennis* and *Urtica dioica* are not grazed. In a few bare patches species of *Cladonia* and *Parmelia* are present and slowly increasing.

No. 6. PENTLAND HILLS

The general vegetation was a mixed heath type of *Calluna-Vaccinium-Nardus-Festuca-Agrostis. Calluna vulgaris* is rapidly disappearing, *Nardus stricta* and *Vaccinium Myrtillus* will suffer next, and later, grazing will affect *Agrostis* spp., *Festuca ovina*, and *Deschampsia flexuosa*. At present *Agrostis-Festuca-Deschampsia* is spreading, as well as *Galium saxatile* which is not grazed. Recently there has been a noticeable increase in moss and lichens. These appear as *Calluna* and *Vaccinium* slowly die. The most common mosses were *Hylocomium squarrosum, Hypnum Schreberi*, and *Dicranum scoparium.*

No. 7. PENTLAND HILLS

This was formerly typical heathy grassland with a little *Pteridium aquilinum.* The vegetation now consists of an *Agrostis-Festuca* Association (d.) with *Deschampsia flexuosa* (a.), *Holcus mollis, Deschampsia caespitosa, Galium saxatile, Veronica chamaedrys, Achillea millefolium, Cerastium semidecandrum, Rumex Acetosella, Hieracium pilosella* and a little of *Poa annua* and *Aira praecox. Holcus mollis* is slightly grazed as is *Hieracium pilosella.* All other plants are grazed except *Galium saxatile.* *Deschampsia caespitosa* is severely grazed. *D. flexuosa* is still spreading as *Agrostis-Festuca* is being slowly suppressed. *Galium saxatile* is spreading very rapidly, being ungrazed and lying very prostrate.

No. 8. PENTLAND HILLS

The vegetation was a typical heath grassland with a little *Vaccinium Myrtillus*. It is now *Agrostis-Festuca* grassland with *Nardus stricta, Deschampsia flexuosa* and *D. caespitosa, Potentilla erecta, Pteridium aquilinum* (a few small clumps), *Cnicus arvensis, Viola canina, Galium saxatile, Holcus mollis* and *H. lanatus*. It is interesting in this case that *Pteridium aquilinum* has been slightly grazed as are both species of *Holcus* and *Cnicus arvensis. Deschampsia flexuosa* and *Galium saxatile* are both spreading and co-dominant but the former is being grazed so that in time *Galium saxatile* will no doubt assume a dominant role. Since both of these plants spread at the expense of the *Agrostis-Festuca* grassland it is merely a matter of time ere *Agrostis-Festuca* becomes of little importance. Mosses are beginning to spread through the vegetation, and *Vaccinium Myrtillus* is rapidly disappearing.

No. 9. MOORFOOT HILLS

The vegetation was a formerly typical Callunetum with some *Vaccinium Myrtillus. Calluna vulgaris* and *Vaccinium Myrtillus* have been suppressed by rabbits and an *Agrostis-Festuca* grass heath has been formed with *Deschampsia flexuosa* present. As the burrows are rather scattered pressure has not been very severe, so that a good grassy type of vegetation still remains.

NO. 10. MOORFOOT HILLS

Rabbits had invaded an old retrogressive open birch wood. Originally the ground vegetation had been *Calluna vulgaris* with a little *Vaccinum Myrtillus*. As usual under rabbit influence *Calluna vulgaris* has been cleared in many places, and *Vaccinium Myrtillus* is also disappearing. *Agrostis-Festuca* grassland has succeeded the Callunetum accompanied by *Galium saxatile* and a little *Deschampsia flexuosa*. Other plants present are *Rumex acetosella, Deschampsia caespitosa, Potentilla erecta, Digitalis purpurea, Urtica dioica, Myosotis versicolor, Poa annua, Cnicus lanceolatus* (a few plants), and *Hypnum Schreberi* is the chief moss. A few plants of *Erica cinerea* are present. In the present example none of the miscellaneous plants showed signs of grazing.

NO. 11. MOORFOOT HILLS

In the original vegetation *Vaccinium Myrtillus* was dominant and *Calluna vulgaris* subdominant. These two plants have been grazed off near the burrows and replaced by an *Agrostis-Festuca* grassland with *Deschampsia flexuosa* (a.) slowly spreading accompanied by *Galium saxatile*. In the grassy areas *Agrostis* spp. are dominant and *Festuca ovina* agg. subdominant. Other plants present are *Viola lutea, Plantago lanceolata, Deschampsia flexuosa, Carex* spp., *Potentilla erecta, P. fragariastrum, Luzula campestris, Thymus serpyllum, Hieracium pilosella, Urtica dioica, Hypnum Schreberi* and *Dicranum scoparium*.

NO. 12. MOORFOOT HILLS

The vegetation was a typical Callunetum and the rabbit population was not dense. *Calluna vulgaris* was reduced in places to isolated clumps, and these were decaying with lichens present. Now, *Agrostis-Festuca* is dominant between the remaining tufts of *Calluna*, and locally moss is spreading as well as *Galium saxatile*. *Cladonia rangifera* is abundant in bare places, with patches of *Hylocomium triquetrum*.

NO. 13. MOORFOOT HILLS

The vegetation consists of short dense *Calluna vulgaris*, scattered and very small patches of *Pteridium aquilinum, Ulex europaeus* (apparently dying out), *Agrostis-Festuca, Helianthemum vulgare* (f.), *Thymus serpyllum, Viola tricolor, Potentilla erecta, Luzula campestris, Dicranium scoparium*, and a few birch seedlings. The rabbit pressure is killing *Calluna vulgaris* and it is being replaced by *Agrostis-Festuca* with a mere trace of *Deschampsia flexuosa*. *Pteridium aquilinum* is invading some of the grassy patches which replaced *Calluna vulgaris*. Moss, chiefly *Hylocomium squarrosum*, is steadily spreading through much of the grass. *Galium saxatile* is absent.

No. 14. MOORFOOT HILLS

The vegetation in this example was a mixture of *Calluna vulgaris* and grass with thinly scattered *Pteridium aquilinum*. The grassland part is spreading and consists of *Festuca-Agrostis* with *Deschampsia flexuosa*. Other plants present are *Luzula campestris*, *Carex* (including *C. glauca*), *Potentilla erecta*, *Veronica serpyllifolia*, *Rumex Acetosella*, *Trifolium minus*, *Galium saxatile*, *Teucrium Scorodonia*, *Nardus stricta* (o.), *Hypnum Schreberi*, *Polytrichum juniperinum*, *Cladonia rangifera*, *Cladonia pyxidata*. The rabbit pressure is gradually destroying *Calluna*, then depressing the grassland to a *Deschampsia flexuosa-Galium saxatile* community, and in extreme parts to a moss-lichen vegetation with only a little *Galium saxatile* and *Deschampsia flexuosa* left.

No. 15. MOORFOOT HILLS

Here *Calluna vulgaris* heath is rapidly changing to *Agrostis-Festuca* grassland with much *Galium saxatile* scattered through the grass. *Pteridium aquilinum* occurs in isolated patches with *Oxalis Acetosella* in its shade, and a little *Holcus mollis*. Other plants present are *Ajuga reptans*, *Potentilla fragariastrum*, *Myosotis collina*. The chief changes are the increase of grass and the spread of *Galium saxatile*. A large influx of rabbits with extensive burrowing has left much bare sandy soil on which *Festuca-Agrostis* and *Galium saxatile* are the chief colonizing plants.

No. 16. MOORFOOT HILLS

The original vegetation was a very mixed heath of *Calluna vulgaris*, *Vaccinium Myrtillus*, *Nardus stricta*, *Festuca ovina*, *Deschampsia flexuosa*, *Agrostis* spp., *Holcus mollis*, *Teucrium Scorodonia*, *Hypericum humifusum*, *Galium saxatile*, *Polygala vulgaris*, *Oxalis Acetosella* (a few plants), *Aspidium Filix-mas*, *Rhacomitrium lanuginosum*, *Dicranum scoparium*, *Hypnum cuspidatum*, *Hylocomium triquetrum* and *Hypnum Schreberi*. Rabbits have altered this rather varied vegetation near their burrows to *Festuca ovina* (d.), *Galium saxatile* (s.d.), both rapidly spreading. Also present are *Polygala vulgaris*, *Agrostis* spp., and lichens identified as *Peltigera canina*, *Cladonia rangifera* and *Cladonia pyxidata*.

No. 17. MOORFOOT HILLS

The original vegetation consisted of *Calluna vulgaris* (d.), *Nardus stricta*, (s.d.), *Erica cinerea*, *Molinia caerulea*, *Deschampsia flexuosa*, and *Polytrichum commune*.

After rabbit grazing, the vegetation became *Nardus stricta* (d.), *Galium saxatile* (s.d.), *Agrostis-Festuca*, *Deschampsia flexuosa*, *Anthoxanthum odoratum* (r.), *Potentilla erecta* and *Erica cinerea* (r.).

No. 18. MOORFOOT HILLS

A vegetation of *Calluna vulgaris*, *Vaccinium Myrtillus* and *Nardus stricta* with traces of *Deschampsia flexuosa*, *Festuca ovina* and *Agrostis palustris* (Hud.) has been altered to *Deschampsia flexuosa* (d.), *Galium saxatile* (s.d.), *Agrostis-Festuca* (r.), *Calluna vulgaris* (r.), *Vaccinium Myrtillus* (r.), *Nardus stricta* and a few plants of *Poa annua.*

No. 19. MOORFOOT HILLS

The original vegetation consisted of a heathy grassland of *Agrostis-Festuca* with *Deschampsia flexuosa*, a little *Calluna vulgaris*, *Vaccinium Myrtillus*, *Nardus stricta*, *Galium saxatile*, *Potentilla erecta* and *Deschampsia caespitosa*. Rabbit grazing has modified this vegetation to *Galium saxatile* (d.), *Deschampsia flexuosa* (s.d.), *Festuca-Agrostis* (o.). *Deschampsia caespitosa* was practically grazed out as well as *Calluna vulgaris*, *Vaccinium Myrtillus* and *Nardus stricta* Also present are a little *Hylocomium squarrosum*, *Ulothrix* spp. on bare ground, but so far no lichens have appeared.

No. 20. PENTLAND HILLS

This example is very interesting as the burrow, though small, is situated near the foot of the north-facing scree of Caerketton, and is in a shaded situation where the sun seldom penetrates even in summer. It is therefore both rather damp and cold, and such examples of this type are rare.

The normal vegetation of the area consists of *Nardus stricta* (d.), *Agrostis-Festuca* (s.d.), patches of *Luzula maxima* (l.a.), *Oxalis Acetosella* (f.), *Galium saxatile* (o.), *Holcus mollis* (o.), also *Hypnum Schreberi*, *Polytrichum commune*, *Plagiothecium undulatum*, *Hylocomium squarrosum*, and *Cystopteris fragilis*.

Rabbit grazing has altered this vegetation to *Agrostis-Festuca-Hylocomium squarrosum* (co.-d.), *Deschampsia flexuosa* (f.), *Galium saxatile* (f.), *Holcus mollis* (f.), *Luzula maxima* (well grazed), a few plants of *Deschampsia caespitosa* (closely grazed) while the other plants previously occurring have disappeared.

No. 21. PENTLAND HILLS

This burrow faces north-east and is on the lower part of an outlier on the western end of Caerketton. This position is in the shade most of the year. The surrounding vegetation is *Nardus stricta* (d.), *Agrostis-Festuca* (s.d.), *Rumex Acetosella* (o.), *Oxalis Acetosella* (o.), *Galium saxatile* (o.), *Deschampsia flexuosa* (o.), *Holcus mollis* (o.), *Plagiothecium undulatum* (l.a.), and *Polytrichum commune* (l.a.).

Rabbit grazing has altered this vegetation to an *Agrostis-Festuca-Deschampsia flexuosa* short grassy turf, with *Galium saxatile* (f.), *Hylocomium squarrosum* (f.), *Urtica dioica* (one small patch), a little *Dicranum scoparium*, and several species of *Cladonia.*

No. 22. PENTLAND HILLS

This burrow is near to no. 21 but faces north-east by north.

The original vegetation consisted of *Vaccinium Myrtillus* (d.), *Nardus stricta* (s.d.), *Agrostis-Festuca* (f.), *Deschampsia flexuosa* (o.), *Oxalis Acetosella* (o.), *Galium saxatile* (o.), *Holcus mollis* and *Polytrichum commune* (l.a.).

This vegetation has been changed by rabbit grazing to *Deschampsia flexuosa* (d.), *Galium saxatile* (s.d.), *Hylocomium squarrosum* (f.), some *Agrostis-Festuca*, and a little *Holcus mollis*.

DISCUSSION

The influence of rabbits grazing on vegetation was first satisfactorily dealt with in a now classic publication by Farrow (1925) who showed how *Calluna vulgaris* was killed out and replaced by a grass-heath type of vegetation. In extreme cases lichens finally replaced other plants. This work dealt with certain parts of the well-known East Anglian heaths. Watt (1936–7), who has done some very careful, intensive, and recent work on Breckland, is not in entire agreement with Farrow's conclusions. Watt considers that the rabbit is not the sole cause of the changes recorded. Be that as it may, rabbits are a very potent force, by their grazing, in altering or modifying the vegetation of any part where they are present in numbers. Moore (1931) gave an account of the secondary succession following rabbit damage in the Isle of Man. The first stage was a lichen stage, the second a moss stage, the third a *Sedum-Carex arenaria* stage and lastly what might be termed a grass-heath stage. All the areas which these three investigators have explored have much in common. Hence it may be thought that no comparison is valid with the results of rabbit pressure on hill grazings. But many parts of hill grazings have distinct resemblances to heaths and their vegetation is often very similar (Fenton, 1936, 1937 *b*). Where the surface vegetation gets too thin or is destroyed, leading to "scree" formation, there is often much in common between the heaths discussed and parts of these hill grazings (Fenton, 1939).

Whether we consider lowland heaths or hill grazings, the first stage is the destruction or partial destruction of the vegetation covering of the soil. This is not always caused by rabbits, but may be due to sheep or even human influence (Fenton, 1937 *a*). In some cases there may be a combination of these factors. But in many places, even in remote parts, rabbits have increased enormously during the last few years. Where rabbits are numerous the vegetation shows very marked changes. Considering the examples quoted it is evident that the approximate order of depression and extinction are (1) *Calluna vulgaris*, (2) *Vaccinium Myrtillus*, (3) *Nardus stricta*, (4) *Agrostis-Festuca*, (5) *Deschampsia flexuosa*. In extreme cases much of the ground may be covered by lichens, chiefly *Cladonia* species, and a varying quantity of mosses. Finally, even the mosses may become scarce. In several places this order of change has been observed over a period of several years. *Deschampsia flexuosa* sometimes disappears before *Agrostis-Festuca* is seriously affected. The sequence of change, or retrogression (agriculturally) is the reverse process of what Moore (1931) described for the Ayreland of Bryde, Isle of Man. It is also of interest that in the dune area near Gullane on the Firth of Forth there are thin vegetation coverings which consist largely of lichens and mosses. This area is heavily grazed by rabbits, as the large number of droppings indicates. For many years this vegetation has shown no real change and may be regarded as a biotic climax. So far, nothing in the nature of a blow-out such as those described by Watt (1936) in Breckland, has been observed, except in open dunes next the Forth. Consequently the thin sand and its inability to supply moisture or humus, does not permit a stronger growing vegetation such as begins to form as one passes away from the coast inland towards the Golf Links. Some grasses and other plants do commence growth, but they are grazed and soon afterwards die out. It would therefore seem that the lichen-moss → heath grass may be a reversible process, and may continue in various states of equilibrium for an indefinite time. Nos. 4, 12, 13, 14, 16 very definitely show that hard grazing by rabbits, leading to almost total destruction of the original vegetation, can produce the moss-lichen stage and occasionally the last or lichen stage.

The general effect of grazing by rabbits may at times be modified by the plants present. *Digitalis purpurea* was readily grazed while the leaves were still young. Older leaves were seldom touched. This is interesting since *Digitalis purpurea* is regarded as a poisonous plant in agricultural circles. *Urtica dioica* was not grazed. This was remarked on by Jeffreys (1917) and Adamson (1921). *Holcus mollis* seems also largely but not entirely immune from rabbit grazing, again largely in agreement with the conclusions of Jeffreys (1917). *Agrostis* and *Festuca* are both grazed but the intensity of grazing varies in different places, doubtless depending on the quantity of suitable food available. *Galium saxatile* does not seem to be grazed as a general rule. That is the chief reason why it spreads and often becomes the dominant plant around and near rabbit burrows. *Galium verum* is also little affected, as where it occurs it generally succeeds in producing a number of inflorescences, which are quite normal though often rather prostrate. *Luzula campestris* is seldom grazed, and is often left untouched. Mosses are grazed to a limited extent, and do not appear to be very palatable to rabbits. Sheep at times will eat considerable quantities of moss. *Pteridium aquilinum* is seldom touched although we have found rabbit damage, for example no. 8. A very complete list of plants avoided by rabbits is given in *The British Islands and their Vegetation* (Tansley, 1939). It is evident from the examples considered that rabbits may be forced to graze unpalatable plants if there is insufficient food in the vicinity. The unpalatable plants may include certain plants normally regarded as poisonous. The amount of any poisonous plant necessary to cause death varies not merely within the same species, but very greatly with different animals. This is well known even among the ordinary animals of a farm. It is hardly possible to draw any satisfactory comparison between the rabbit-grazed chalk grasslands (Tansley, 1922; Tansley & Adamson, 1925) and hill grazings in Scotland, since conditions are so different. The writer noted quite recently, however, that in some of these chalk areas, where *Calluna vulgaris* still clings on precariously, that it is being steadily reduced by rabbits, although sheep also play a part. Without a long continuous study of these chalk land areas, however, it is quite unsafe to try and assess the change from the original vegetation, and allocate due influence to sheep, rabbits or other animals. Many may consider that rabbits grazing near their burrows may not do a great deal of damage, particularly in hill grazings. That is an erroneous conclusion, for it is not the size of each colony and its immediate grazing ground that is significant. The real significance is that the total areas affected by burrows etc. within one valley, hill side, or farm, reaches at times a surprising figure. Rabbits not merely eat the food of sheep or cattle, but they foul much of the herbage with their droppings, and heavy dunging by rabbits is quite sufficient to kill out *Calluna vulgaris*. Examples of this can be found in many parts of hill grazings. It has been estimated that the total annual rabbit damage for Great Britain is £70,000,000. Undoubtedly much, if not most, of this damage is done on farms, but a fair proportion can be debited to rough and hill grazings. Let it not be forgotten that it has been stated that five rabbits account for as much as one sheep (Hume, 1939). If this calculation is correct, then in some parts the sheep population, or its equivalent, could be doubled. It was stated at Dauntsey's School that four rabbits and their progeny have reduced the amount of herbage in one-eighth of an acre by 81·5% in 15 months (Thomas, 1935–7). Another interesting feature was the marked increase in moss till it amounted to half the vegetation. "Leave a pair of rabbits to breed freely and, barring deaths, their progeny in two years may number 800; and, they say, forty rabbits eat as much as a cow" (*News and Notes for Farmers*, 1939). The economic importance of these facts needs no stressing.

There is one other aspect of this rabbit damage. As pointed out elsewhere (Fenton, 1939), rabbits are not merely modifying or altering existing vegetation, but are by their burrowing forming "screes". This is very easily done where stones lie near the surface of the soil. Under such circumstances the "scree" is formed by the removal of small stones which gradually roll down the hill side burying much of the vegetation lying immediately below the burrows. In time with the undermining of much of the slope, parts of the surface collapse, and following heavy rains much of the material gets washed down to a lower level. The vegetation of such "screes" has been dealt with in an earlier publication (Fenton, 1939). Once a burrow becomes a scree the rabbits change their quarters, and in this way continuous erosion is being caused.

Naturally the dominance, co-dominance, or subdominance of various plants will depend largely on the vegetation before rabbits made their presence felt. Thus an *Agrostis-Festuca* association will tend to be replaced by other plant communities or plants (e.g. *Galium saxatile* or *Deschampsia flexuosa*), but if *Calluna vulgaris* is dominant then *Agrostis-Festuca* will most likely be the next phase of "retrogression" (agriculturally) of the vegetation process. Keeping these facts in view a brief analysis of the examples is interesting.

Deschampsia flexuosa is dominant in nos. 1, 2, 18 and 22 (4); co-dominant in nos. 6, 7, 8, 14 and 21 (5) and subdominant in nos. 10, 11 and 19 (3); *Galium saxatile* is dominant in nos. 3, 14 and 19 (3); co-dominant in nos. 5, 8, 10, 14 and 15 (5) and subdominant in nos. 1, 2, 6, 16, 17, 18 and 22 (7). Taking *Agrostis-Festuca* as a unit, this well-known association is dominant in nos. 9, 11, 12, 13 and 16 (5); co-dominant in nos. 5, 6, 7, 10, 15 and 21 (6); and subdominant in nos. 3 and 4 (2). *Nardus stricta* is dominant in no. 17. Moss is subdominant in nos. 12 and 13, and present in nos. 6, 8, 10, 11, 14, 16, 18, 19 and 20. In other words, moss is present, often in quantity, in half the examples selected. Lichens are present in nos. 4, 5, 6, 12, 14 and 16. Nearly one-third of the examples have lichens present, some of them in quantity. In ten of the examples *Deschampsia flexuosa* is present in quantity, this is also true for *Galium saxatile* in fourteen, for *Agrostis-Festuca* in twelve, and moss in two. These figures summarize the position with regard to the importance of the most frequently occurring plants. *Deschampsia flexuosa* occupies a peculiar position. Normally this grass is most frequent in colonizing bare peaty soils and places where soil erosion has occurred. It is very frequent, following burning of heather or the felling of pine woodlands. In this respect it is ephemeral, since, with the formation of a satisfactory covering of vegetation, *D. flexuosa* dwindles often to a few plants. Its frequence in so many of these rabbit-infested areas is filling up gaps between the various phases of succession (or retrogression). No distinction has been made between *Agrostis palustris* Huds., and *Agrostis canina* with *Festuca ovina*, because the dominance of *Agrostis* or *Festuca* readily alters according to circumstances (Fenton, 1934). *Agrostis-Festuca* association is the general type of grassland which follows *Calluna vulgaris* heath (on hillsides) when the grazing of sheep gradually suppresses *C. vulgaris* and *Vaccinium Myrtillus*. *V. Myrtillus* often lingers long, and may survive indefinitely, depending on the grazing pressure. With its well-protected root system and less combustible growth, *V. Myrtillus* generally survives burning, and shortly after begins vigorous growth. *Galium saxatile*, with its prostrate growth, is never present in any quantity if the vegetation is not short. The shorter the vegetation becomes with grazing the more favourable conditions become for *G. saxatile*, for it is seldom grazed. That is why it becomes so plentiful on bare ground or amid short impoverished grass.

The vegetation around rabbit burrows in shade or in northern positions shows the same general trend as those of other situations. As previously pointed out, these burrows are generally small, and it is comparatively rare that burrows occur in damp or shady spots. It may be that rabbits first settled there during dry spells and have remained, otherwise it is difficult to understand why rabbits should choose such places for burrows. The two points of interest are the rapid destruction of those plants generally associated with woods or shady places, and secondly, how the shortening of the vegetation, by the close grazing, tends to dry out the surface soil. This drying effect kills such moisture loving types as *Plagiothecium undulatum* and *Oxalis Acetosella.*

The differences shown in the vegetation of the examples selected are due to several factors. If the burrow is small there is generally sufficient food, and even choice of food, hence the pressure in the vegetation may be slight. As the pressure increases so does the vegetation alter, till all the more "susceptible" plants may be extinguished. Another point of great importance is the amount of moisture available. If the rainfall is sufficient and evenly distributed or there is a "flush" near the burrow, then much, if not most of the vegetation will withstand the attack of the rabbits. Along the eastern parts of the Moorfoots and most of the Pentland Hills there are often dry periods which slow down or arrest growth, so that recovery tends to be slow or delayed, and may in some cases of prolonged drought be completely arrested. The intensity of sheep grazing also can affect the problem, since if the stocking of sheep is heavy then the vegetation is, or may be, well grazed before rabbits begin to make their presence felt. If there was very extensive overgrazing by these two animals it might easily lead not merely to soil exhaustion, but to soil erosion on a considerable scale. The economic importance of such a possibility needs no emphasizing. The rabbit problem has reached the same national danger as the bracken problem (Long & Fenton, 1939). Under present conditions and the dire necessity of producing more food, it does seem rather inconsistent to encourage ploughing up grassland, and make no concerted effort to control the rabbit menace. Otherwise, in many parts the rabbits will benefit more than human beings.

SUMMARY

The areas investigated lie in the Pentland Hills and the northern part of the Moorfoot Hills.

Typical examples of changes in the vegetation due to rabbit grazing are given and comparison is made with the results of other investigators, in particular with Breckland and the Isle of Man.

The plants recorded as unpalatable to rabbits are in agreement with previous findings, except that *Holcus mollis*, *H. lanatus*, and *Pteridium aquilinum* are slightly grazed, and *Digitalis purpurea* is grazed in its younger stages.

The plants which suffer most from rabbit damage are *Calluna vulgaris*, *Vaccinum Myrtillus* and *Nardus stricta*. *Deschampsia caespitosa* where it occurs is quickly destroyed.

D. flexuosa and *Agrostis-Festuca* grassland are both severely grazed, but they are capable of withstanding grazing pressure for a long time. Heath or

mixed heath-grassland is succeeded by an *Agrostis-Festuca* association. This in turn is succeeded by an increase of *Deschampsia flexuosa*, often to a temporary dominance, followed by abundance of *Galium saxatile*. In time there develops a moss-dominated vegetation which in extreme cases degenerates to a vegetation rich in lichens, chiefly *Cladonia*.

Much depends on the density of the rabbit population. The denser it is the more intensive the grazing and the more drastic the vegetation changes.

All vegetation grazed by rabbits was previously grazed by sheep, hence a rabbit-biotic-climax is being superimposed on a sheep-biotic-climax.

Where rabbits are plentiful "scree" formation and soil erosion may occur.

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OBITUARY

HENRY CHANDLER COWLES, 1869–1939

(*With Plate* 25)

Henry Chandler Cowles was one of the two great American pioneers of dynamic plant ecology—the other being F. E. Clements—to whom English ecology owes so much. It is interesting to learn that he, like the present writer, was originally inspired by Warming's *Plantesamfund* (Copenhagen, 1895) in its German translation by Knoblauch, *Lehrbuch der ökologischen Pflanzengeographie* (Berlin, 1896). It was the conception of a "Pflanzenverein"—which we now call in English a "plant community"—and its determination by habitat there set forth, together with his own training in physical geology that led Cowles to the dynamic conceptions of vegetation which he applied in so masterly a manner in his classical study, "The ecological relations of the vegetation on the sand dunes of Lake Michigan" (*Bot. Gaz.* 1899). This he followed, two years later, by a more general application of the same ideas to the whole Chicago region in "The physiographic ecology of Chicago and vicinity" (*Bot. Gaz.* 1901). On the same subject he afterwards published general papers, "The fundamental causes of succession among plant associations" (Brit. Assoc., Winnipeg, 1909) and "The causes of vegetative cycles" (*Bot. Gaz.* 1911).

The first two of these papers laid the foundations of the modern theory of vegetational succession, a process which was worked out in great detail for a particular "hydrosere" by one of Cowles's pupils, W. S. Cooper, in "The climax forest of Isle Royale, Lake Superior, and its development" (*Bot. Gaz.* 1913); and it is on these foundations (together with Clements's publications, *The Development and Structure of Vegetation* (1904), *Research Methods in Ecology* (1905), and the monumental book *Plant Succession* (1916) propounding an elaborate system of successional phenomena and a close analysis of its causes) that subsequent work on dynamic ecology has been based.

Cowles was a New Englander, born at Kensington, Connecticut, in 1869 and receiving his early education in the State schools and in the New Britain High School. Later he entered Oberlin College and took his bachelor's degree in 1893. For two years he taught at Gates College, and in 1895 went to the University of Chicago where he held a fellowship and studied geology with deep interest; but on the appointment of John Merle Coulter in 1897 as Professor of Botany Cowles was attached to the newly organized Department of Botany as an assistant, and became one of the brilliant little group of botanists that Coulter gathered round him. In 1898 he received the degree of Ph.D. for his fine pioneer work on the vegetation of the Lake Michigan dunes.

Cowles remained at the University of Chicago for the rest of his working life, becoming professor in 1911 and chairman of the department in 1925, a position he held until his retirement in 1934. Of his many activities and distinctions, a few only need be mentioned here. In 1910 he was president of the Association of American Geographers and in 1917 of the Ecological Society of America, organized in 1914 largely through his efforts and of which he was the first secretary-treasurer. In 1922 he was president of the Botanical Society of America, and in 1930 his status as one of the great pioneers in the field of dynamic plant ecology was publicly recognized in England by his appointment as president of the section of Phytogeography and Ecology at the International Botanical Congress at Cambridge.[1] In 1934 he was made an honorary life member of our Society, of which he was an ordinary member from its foundation in 1913. Cowles's training in geology and his keen, abiding interest in the causation of the physical features of landscape and their relation to vegetation had a decisive effect on his pioneer work and on the whole of his subsequent teaching and activity. At the University of Chicago he inspired and trained many original investigators of American vegetation, among whom may be mentioned V. E. Shelford, the distinguished animal ecologist, H. L. Shantz, W. S. Cooper, G. D. Fuller, and the late G. E. Nichols. And his influence was by no means confined to America. It was felt in Europe and especially in Great Britain, where it was an important factor in the development of British plant ecology. It is interesting to note that the late C. B. Crampton—whose life was prematurely cut off at an early age—was also a field geologist by training (and profession), and arrived independently, 10 years later, at some of Cowles's views on the dynamic aspects of vegetation, though in complete ignorance of Cowles's work.

Like Carl Schröter, whose loss we mourned earlier in 1939, Cowles was essentially a field teacher, whose excursions were a vital part of his teaching, and on these, like Schröter, he was always the centre of a crowd of enthusiastic and devoted students. Like Schröter, too, he was a man of infectious gaiety and high spirits and of infinite humanity and humour, a loyal and affectionate friend who never spared himself in giving help, and always quick and generous in his appreciation of the good work of others.

The last decade of Cowles's life was overshadowed by serious illness, which eventually put an end to his powers of active work. In 1930, when he visited England with his wife and daughter for the International Congress, he was no longer quite his old self, though still keenly interested in what we could show him. Hence the contemporary portrait, which is reproduced on the accompanying plate, does not do justice to his vital and charming personality. This is better shown in the enlarged heads below, which are extracted from groups taken on the International Phytogeographical Excursions through the British Isles in 1911 and in the U.S.A. 1913, of which he was an outstanding figure.

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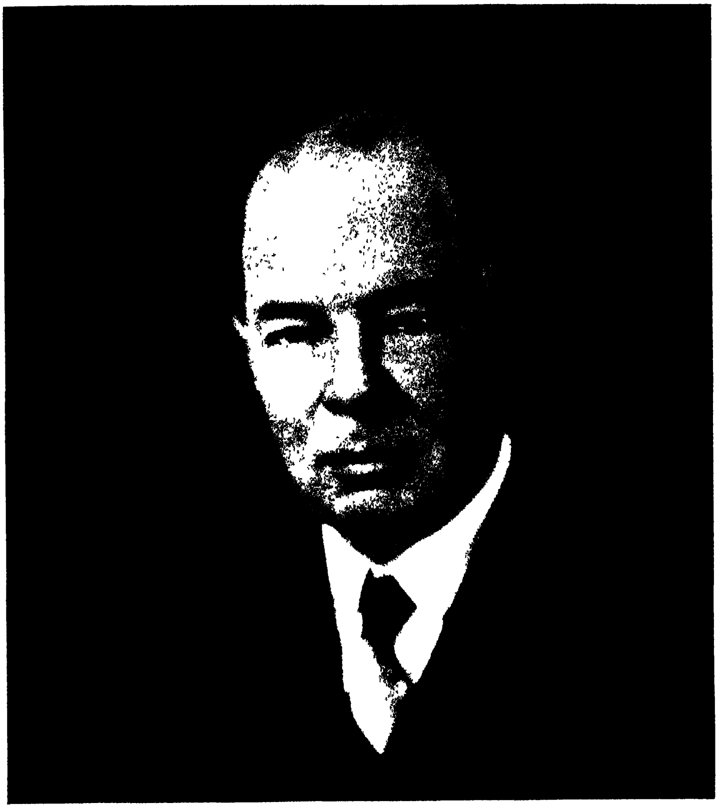
[1] For most of the facts of Cowles's career we are indebted to Prof. G. D. Fuller's obituary notice in *Science*, **90**, 363–4, 1939.

After his retirement in 1934 his American colleagues and friends arranged for the July 1935 issue of *Ecology*, the journal of the Ecological Society of America, to be devoted to a collection of papers by his pupils and colleagues, both in America and abroad, in honour of Cowles. The announcement of this scheme brought responses from more than 300 people, "and with almost every contribution came a letter expressing admiration for Cowles...." The "Festschrift" was in fact a fine monument to the universal esteem and affection in which he was held.

Cowles's achievement is fitly summarized in the words of Prof. W. S. Cooper, one of the ablest of his old pupils: "He laid the foundation for a new and useful branch of science, he constructively influenced the thought of hundreds of investigators and teachers, and in his professional and personal contacts he made for himself a multitude of devoted friends." A. G. T.



1930

Grantchester, 1911

Connemara, 1911

Rocky Mountains, 1913

HENRY CHANDLER COWLES

A SANDY AREA IN THE DOVEY ESTUARY

By J. M. LAMBERT and M. R. DAVIES

(*With three Figures in the Text*)

The main features of the Dovey estuary have already been fully described, both in relation to the topography and to the vegetation (**1**, **7**, **11**, **12**, **13**). In recent years, however, certain developments, which appear to be worthy of record, have taken place at the seaward end of the estuary, in the lee of the main dune system projecting from the southern bank and extending partially across the river mouth. The particular interest of this region lies in the fact that these seaward dunes have been broken through by wind action at the south-west corner of the area, and a small dune is gradually forming in direct line with the passage of the prevailing wind from blown sand carried in through the gap. This new dune is developing on an area that was formerly almost entirely covered by most spring tides, and the lower parts of the area are still periodically submerged and bear typical salt-marsh plants such as are found in the more muddy marshes further up the estuary. Even in those parts not

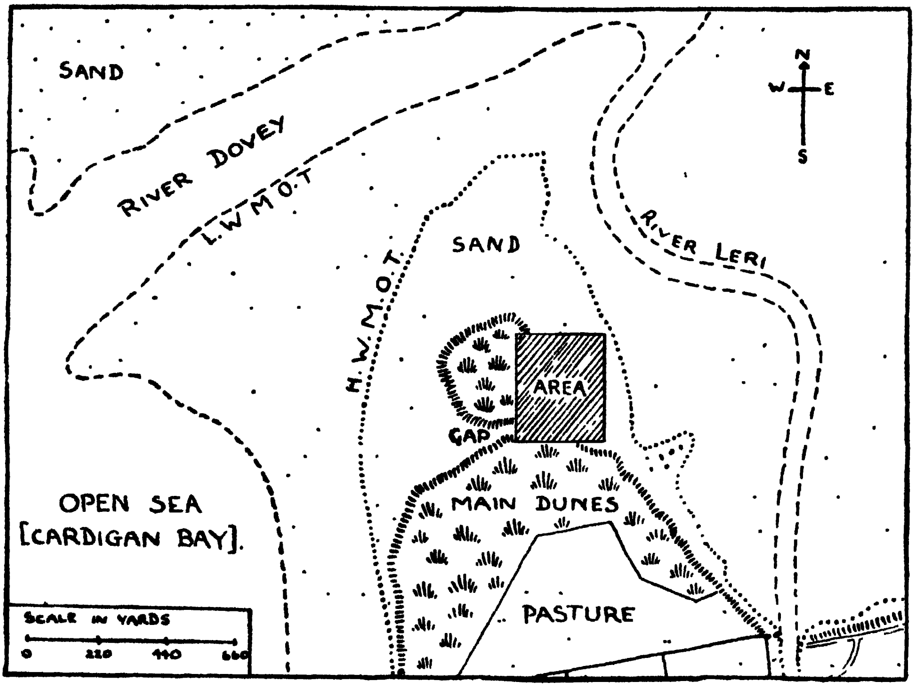


Fig. 1. Sketch map to show the relation of the area to the main dune system.

directly in line with the prevailing wind, sufficient blown sand is distributed over the area to have a very considerable effect upon the nature of the substrate, giving especial interest to the composition and relations of the salt-marsh vegetation of these lower parts.

The area under consideration, excluding the more mature dunes bounding it on the south and west (seaward) sides, is approximately 27 acres in extent. Of this, a little more than half is actually under vegetation. The young dune itself occupies about 2 acres, and bears an almost pure covering of *Triticum junceum*, although in places *Salsola Kali* becomes co-dominant. Other isolated dune or strand plants occur, such as *Euphorbia Paralias*, *Eryngium maritimum*, *Arenaria peploides*, and *Atriplex hastata* var. *prostrata*. *Cakile maritima* seedlings also establish themselves annually upon the dune, although it may be recorded that a single exceptionally high summer tide of June 1938, which submerged even the top of the young dune, appeared to be responsible for the complete elimination of this plant from the inundated area for that year, the associated species being relatively unaffected.

It appears, however, to be exceptional for the entire *Triticum* dune to be submerged by a high tide, although water flows completely round it at most of the higher spring tides. There is another large tract of *Triticum* on the western side of the area under the shelter of the seaward dunes. This does not accumulate blown sand to such an extent; it is consequently at a lower level and is more frequently submerged, although, even so, it is only affected by spring tides, or by ordinary tides brought to unexpected heights by exceptional meteorological conditions. In contrast to the dune plants associated with the *Triticum* of the young dune, its associates on this lower area are *Glaux maritima*, *Glyceria maritima*, and even, in parts, *Salicornia europaea*.

A similar community may be seen on the eastward side of the *Triticum* dune. At the edge of this, *Glaux* becomes in parts co-dominant with the *Triticum*, but at lower levels, the *Triticum-Glaux* community gives place to *Glaux-Glyceria*, then to pure *Glyceria* tussocks, and eventually to a very poor open association of *Salicornia europaea*. Together with the *Salicornia*, one or two clumps of *Spartina Townsendii* occur; these probably originated from the plants introduced higher up the estuary in 1920 (**14**). The occurrence of *Spartina* on this area is of particular interest in relation to the very sandy nature of the substrate, since it is typically a plant of soft tidal muds (**5**).

Of the other low-lying areas, *Glaux maritima* is the dominant plant, especially in those parts where surface water tends to accumulate. In two zones, the small decumbent plants occur thickly enough to form a definite sward, and it is particularly significant that these two areas are relatively poorly drained, especially the more easterly one. Tidal water of the higher spring tides enters this latter zone at the upper end, but on retreat of the tide water accumulates at the lower end, which is enclosed by raised banks of *Triticum* and where there no drainage outlet, the water escaping only by percolation through the soil.

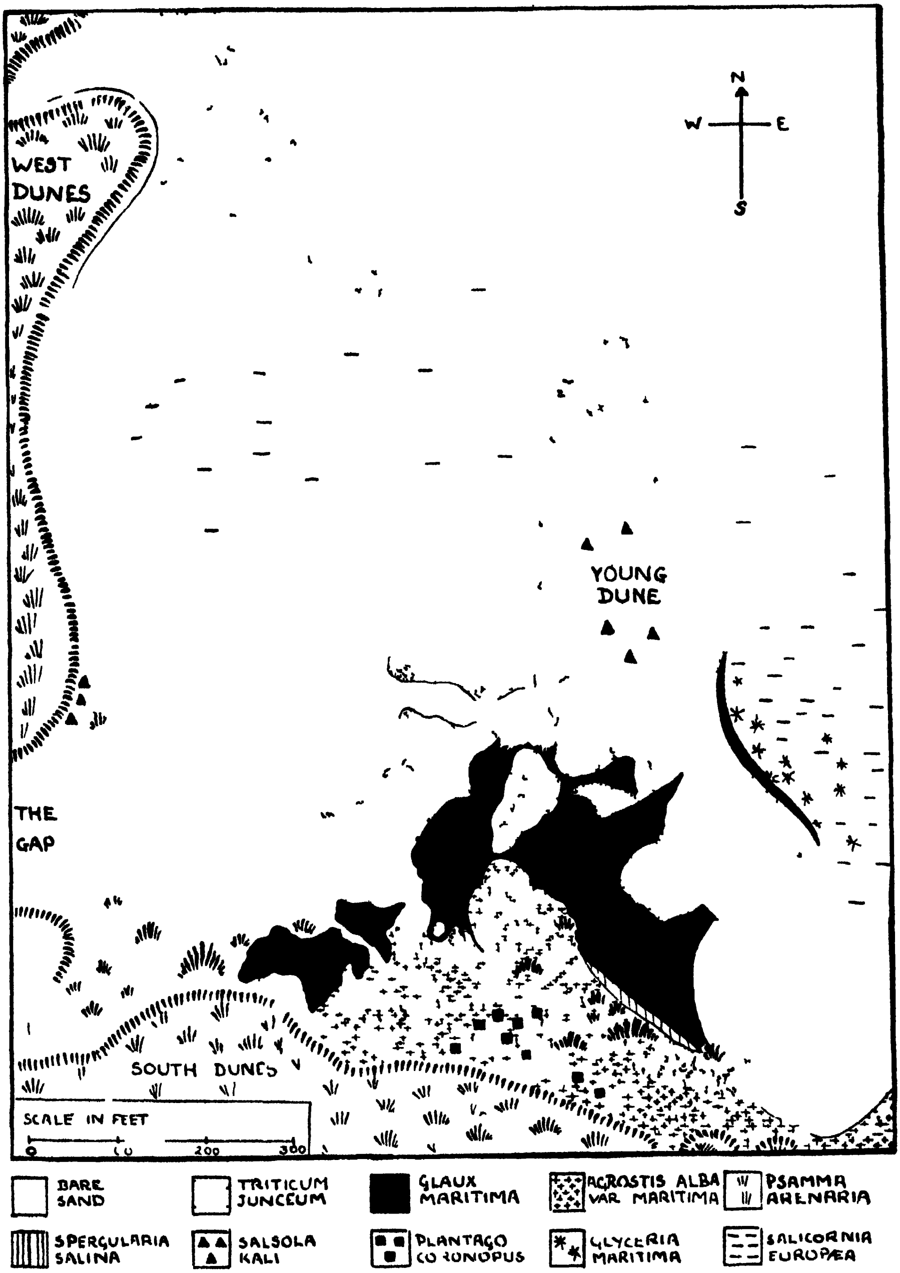


Fig 2 Vegetation map of the area showing the dominant plants of the different communities

Rain water also accumulates in the same way, to such an extent that from the beginning of October 1938 until February 1939 an extensive pool of surface water was continuously present. Such a long period of submersion is however probably exceptional, and may be correlated with the particularly high rainfall of this period as compared with the average monthly figures, although even during very warm and dry summer weather, water which had accumulated in this area after the high tide of 28 June 1938, took four days to disappear completely.

The occurrence of *Glaux* so extensively on these poorly drained areas may be correlated with several other records, perhaps one of the most interesting being the invasion by this plant of certain undrained "high-level" pans of the main Dovey marshes (**12**). A similar state of affairs is indicated at Talsarnau (**13**), where *Glaux* is again the first colonizer of undrained pans. A further comparison may be made with certain of the "lows" at Blakeney Point (**4**); these depressions between two adjacent beaches are accessible to exceptionally high spring tides, and are also liable to flooding by rain water, and one such "low", appropriately designated the "*Glaux* Low", is characterized by an almost pure carpet of this plant. An additional similar locality is described by Stocker (**8**), who records *Glaux* as occurring abundantly in the sandy flats between the dunes at Darss.

The *Glaux* plants of the investigated area at the mouth of the Dovey are interspersed with scattered *Glyceria maritima* tussocks, and one or two of these bear a small patch of *Festuca rubra* at the apex, a miniature reproduction of the well-marked zonation seen higher up the estuary. The tussocky habit of these grasses here may be contrasted with the firm level sward characteristic of the Glycerietum and Festucetum of the main Dovey marshes.

In the upper parts of the main *Glaux* zones, *Armeria maritima*, *Plantago Coronopus*, and *Juncus Gerardi* occur frequently, and also a very few isolated plants of *Suaeda maritima* (a species which is often recorded as abundant on other sandy marshes). On one small strip, somewhat higher and better-drained than the rest, the *Glaux* gives place to *Spergularia salina*, becoming itself only subordinate in that part. These upper *Glaux* zones may perhaps be said to correspond to the Armerietum of the main Dovey marshes, and it is interesting to note that, whereas on the muddy marshes higher up the estuary *Glaux* appears as a subordinate species in relation to the *Armeria*, on the sandy substrate their mutual relations are the reverse. This may quite probably be accounted for by the poor drainage of these particular zones, since both Wadham (**9**) and Morss (**3**) comment on the fact that prolonged periods of immersion are unfavourable to *Armeria*, and that it fares badly on water-logged areas that may at times have a high salt content.

The *Juncus maritimus* zone, which is so prominent higher up the estuary, is here only represented by one or two isolated patches. Instead, with rise in level from the main *Glaux* zones to the mature dunes on the south side, the series appears to be from *Glaux* and its associated plants, through *Agrostis alba* var. *maritima*, with *Plantago Coronopus* locally dominant, to a strand community, with *Carex arenaria* and *Euphorbia Paralias*, mixed with abundant *Agrostis*. *Glaux* is still locally dominant in depressions, two fairly extensive patches occurring here. *Erythraea Centaurium* is also frequent here, although existing plants were destroyed by the same high tide as that which accounted for the disappearance of *Cakile* on the young dune; however, as in the case of *Cakile*, the following year found seedlings again firmly established.

The strand community is relatively narrow, and merges quickly into the edge of the mature marram dune. Isolated patches of marram appear to be encroaching on the area from these south dunes, but at present none of these have yet established themselves on the young *Triticum* dune.

In the investigated area, as in other regions of the Dovey estuary (**1**), the algae as a whole play a very subsidiary part in relation to the phanerogamic vegetation. There is however a certain sparse "permanent" algal component, in contrast to the abundant drift-weed. On the lower reaches to the east and west of the *Triticum* dune, blue-greens are the more common, with *Microcoleus cthonoplastes* dominant, and *Oscillatoria* spp. frequent. In the higher, though somewhat wetter, *Glaux* zones, the blue-greens are largely replaced by green algae, among which the dominant position is held by various species of either *Vaucheria* or *Enteromorpha*, with *Rhizoclonium implexum* also abundant among other subsidiary species. Such algae as are present appear to undergo a seasonal periodicity in their development, reaching a maximum in November, during which month a comparatively prominent algal felt becomes apparent in certain zones. Chapman, finding a similar late autumnal maximum on the Norfolk marshes (**2**), suggests that this may have some correlation with low chloride values of the surface layers of the soil during the winter months.

The vegetation of the whole area, as is the case for the salt-marshes almost throughout the length of the Dovey estuary, is subject to grazing by both sheep and rabbits. The *Triticum* does not appear to be very much affected by this, and flowers profusely in the summer, especially at the lower levels, but other grasses, such as *Glyceria*, *Festuca* and *Agrostis*, are closely cropped. In the marshes higher up the estuary, *Juncus maritimus* plays a relatively important part in the zonation. This plant, owing to its unpalatable nature, is immune from grazing, and hence its relatively tall growth affords a certain protection to other plants associated with it; such plants therefore attain a comparatively luxuriant habit within the Juncetum. The *Juncus maritimus* community is however very poorly represented towards the mouth of the estuary, with the result that the whole of the area is exposed to the depredations of grazing animals.

To make a general comparison of the vegetation of this region with that of the main Dovey marshes, it may be said that in actual floristic composition, the more typically salt-marsh component of the vegetation of the investigated area, though not quite as rich, is very similar to that of the marshes further up the estuary, although the frequency and distribution of the various species, and their interrelationships, are to some extent modified by the particular ecological conditions to which they are subjected. It seems that the same general distributional factors, conjoining to cause the absence or scarcity of certain species and the presence of others, appear to operate throughout the whole estuary. The absence of *Statice Limonium* and *Obione portulacoides* (both of which occur on other Welsh marshes), the comparative rarity of other plants such as *Suaeda maritima*, and the restricted role of *Salicornia* as a primary colonizer, are all features in common with the main muddy marshes.

It is in the higher tidal zones that the chief differences appear, and it is here that the influence of the blown sand is most effective in changing the character of the vegetation. Instead of a Festucetum and a Juncetum, the higher parts are here occupied by an encroaching dune flora, in which *Triticum junceum* plays by far the most important part. *Juncus maritimus* and *Festuca rubra* are almost eliminated, and only occur in isolated patches. The comparatively large vertical range of the salt-tolerant *Triticum* enables it to encroach further on the lower, more frequently inundated, zones, with a consequent modification of the relationships of the original salt-marsh flora in such regions. Thus, on the east side of the young dune, *Triticum* extends down to a level such as is normally occupied by *Armeria*, resulting in an almost entire elimination of the latter from this zone.

It is concluded that the vegetational covering of the area is the result of the interaction of the following two entirely distinct elements:

(1) A basic and characteristically salt-marsh vegetation similar in floristic composition to that of the lower zones in the main Dovey marshes, and largely controlled by the same complex of factors of dispersal and establishment, the actual interrelationships and frequencies of the plants themselves being to a large extent subservient to the peculiar ecological conditions obtaining in the area.

(2) A superimposed advance dune flora which almost entirely replaces the higher salt-marsh communities characteristic of the upper levels of the main Dovey marshes.

The balance existing between these two elements is largely determined by the rate of accretion of new material over the area. This material is derived mainly from two sources, namely, wind-borne sand and tidal deposits. The operation of both these factors was clearly demonstrated at several points, where vertical diggings showed a definite alternation of sandy and silty layers, the more rapid accumulation of the former being seen in the relative proportions of the sand to the silt. This predominating effect of wind-blown sand in the process of deposition must preclude any correlation between the rate of accretion and the height of the ground or the distance from the main river front, such as was demonstrated for the marshes higher up the estuary (7).

Although both wind and tide can be regarded primarily as agents of deposition, yet at the same time they are responsible for a certain amount of erosion, as is indicated in Fig. 3. The apparently open vegetation of the *Triticum* area, where the surface sand is not stabilized by the more deeply situated interlacing rhizomes, allows of some erosion, only partly counteracted by the protective action of the limp, easily embedded leaves. On the other hand, the more superficial stolons of *Glaux*, the tufted habit of *Glyceria*, and the prostrate and rosette habit of such plants as *Spergularia*, *Armeria*, and *Plantago*, are much more effective as sand-binders. This carpet of vegetation found in the lower, more sheltered, areas forms an effective defence against the removal of soil from these parts, and materials deposited there are to a large extent retained. In addition, the denuding effect of rainfall and tidal action in the transportation of loose material from the higher to the lower parts must also be taken into account, especially in the region of the steeper slopes where there is considerable surface drainage as well as percolation. Although the latter action is one which tends towards a general levelling of the whole area, the accretion of sand blown in through the gap on to the *Triticum* dune itself is more than sufficient to compensate for the loss of material to the lower parts, and this is especially so in the summer when the rainfall is slightly less and the spring tides have a smaller range. The resultant cumulative effect of all factors therefore tends towards a general rise in the average level of the area.

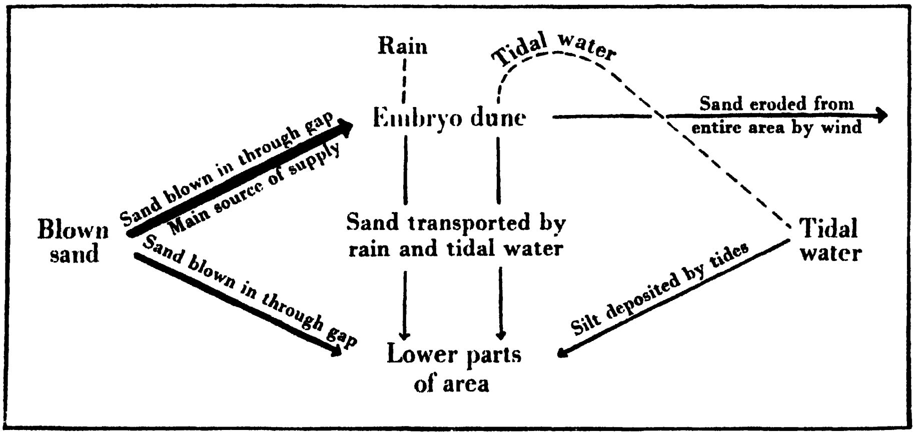

Rain
Tidal water
Embryo dune
Sand eroded from entire area by wind
Sand blown in through gap
Main source of supply
Blown sand
Sand blown in through gap
Sand transported by rain and tidal water
Tidal water
Silt deposited by tides
Lower parts of area

Fig. 3. Diagram to illustrate the interrelationships of the main agents of deposition and erosion of material on the area.

In order to gather a general idea of the variation in the proportion of silt to sand in different parts of the area, a rough mechanical analysis was made of soil samples, taken at successive depths of 7·5 cm., from the *Triticum* dune and from one of the main *Glaux* zones. The high proportion of sand in the soil is indicated by the following figures, which are percentages of air-dry soil:

(1) *Glaux zone*

	Surface	7·5 cm.	15 cm.
By graded sieving—Coarse sand	47·9	70·7	66·0
Fine sand	40·2	27·3	32·9
By difference—Silt and clay	11·9	2·0	1·1
Determined separately—Organic matter	2·4	1·0	1·8
Carbonates	3·3	2·2	1·1

(2) *Triticum dune*

	Surface	7·5 cm.	15 cm.
By graded sieving—Coarse sand	58·8	52·8	47·6
Fine sand	40·5	44·5	52·0
By difference—Silt and clay	0·7	2·7	0·4
Determined separately—Organic matter	1·7	2·2	1·8
Carbonates	2·0	1·4	3·0

The proportion of fine particles is therefore highest in the surface layer of the *Glaux* zone, and this is probably to some extent composed of the fine humic matter formed by the decomposition of the annual aerial parts of the *Glaux* plants; in addition, the relatively poor drainage outlets from this area allow of only a slow recession of tidal water, thus affording ample opportunity for silt deposition.

The following general conclusions have been arrived at from limited observations as to the extent of tidal influence on the area, under normal meteorological conditions:

(1) The area is not affected by tides other than those of the spring cycles.

(2) The *Salicornia-Glyceria* community on the east side of the area is the only one covered by the tides of the lesser spring cycles.

(3) The main *Glaux* zones and the greater part of the lower westerly *Triticum* area are covered by the tides of almost all the major spring cycles.

(4) The higher tides of these major cycles may in addition submerge the lower parts of the *Triticum* dune and the lower reaches of the strand.

(5) It is exceptional for the whole of the area to be inundated, but the maximum tides of the year are sufficient almost to cover both the young dune and the whole of the strand region. Such tides are also the only ones which under normal conditions enter the area through the gap in the seaward dunes as well as from the estuary.

It was frequently found, however, that under different meteorological conditions the relative heights of the tides varied considerably from their estimated values, especially in response to variations in the force and direction of the wind. A general impression was gathered that although a south-west wind may be most effective in increasing the height of the tide on the main coast and in driving water into the estuary, a wind from this direction has less effect in piling up water in this particular corner of the estuary than has a northerly wind (since the main bulk of tidal water approaches the area from the north), unless the south-west wind is of such a force that water is driven in through the gap.

The effect of tidal submersion upon salinity conditions in the area was found to have some relation to the initial depth and salt content of the ground water. Movements of the water table were observed by the use of lengths of drainpipe, covered below by stout cloth and sunk vertically in the sand. It was found that the ground water was not at the same level over the whole area, there being a slight fall from near the mature dunes to areas lying towards low water mark. This gradient is intensified after a period of rainfall, owing largely to increased drainage water from the main dunes. While water level changes due to rainfall operate over the whole area, tidal action only affects those parts which are actually submerged or are within a few yards of the high water mark. At any one point, the rise of the ground water accompanying rainfall or actual tidal submergence is the result of direct downward percolation, and is always more rapid than the subsequent fall due to lateral seepage and evaporation.

The combined incidence of a somewhat greater rainfall and more frequent tidal submersions induces a much higher average level over the whole area during the winter months, and in the low-lying *Glaux* zones, the winter water level is rarely more than a few inches below the surface. The influence of drainage water from the mature dunes surrounding the area maintains the ground water at a fairly low salt concentration in this region, and this is believed to be the chief cause of certain significant differences between salinity conditions in the *Glaux* and *Triticum* zones respectively, emerging from a large number of salinity determinations made on soil samples from different depths and different parts of the area. After a series of winter tidal submergences, the salinity values at successive 7·5 cm. depths in the *Glaux* zone were found to be much lower than those at corresponding depths on the *Triticum* dune. The greater proximity of the comparatively fresh water table and the resultant saturation of the soil in the former region, together with the presence of the somewhat less permeable surface silty layer, are all believed to be effective in offering considerable resistance to the downward percolation of the flooding tidal water, with the result that the values for the layers below the surface, even after several submersions, corresponded remarkably closely to the low values already obtained for the ground water in this part.

In summer, however, when the average water level is considerably lower, very rapid rises in salinity following tidal submersion have been observed in the upper layers of the *Glaux* zones, and in the less well-drained parts, where residual surface water is largely lost by evaporation, it might be expected that warm, dry weather following a high tide would produce very high salinity values, even if these persist only for a short time until the next period of rainfall.

It is the behaviour of the water table that has especial significance in respect to the water relations of the roots of the vegetation. Many of the more typical salt-marsh plants of the lower parts were found to be deeply rooted and able to tap the water table even at its maximum recorded depth, as in the case of *Armeria maritima* and *Juncus Gerardi*, both with roots reaching to a depth of more than 50 cm. Dual purpose root systems occur in other types, notably in *Glyceria maritima*, where the dense mass of adventitious roots at the surface is supplemented by a few much longer roots reaching down to the water table. Other types, such as *Glaux maritima*, *Plantago Coronopus*, *Salicornia europaea*, *Spergularia salina*, and *Suaeda maritima*, exploit the surface layers only, with a root depth of not more than 30 cm. in some species and much less in others, the extension of the root system being mainly lateral.

The root systems of the dune species were seen to be chiefly of the more superficial types, as in *Salsola Kali*, *Cakile maritima*, and *Atriplex hastata* var. *prostrata*. A peculiar feature of the latter is the single particularly long horizontal root which diverges from the main network of roots, and which was found in every specimen examined.

An exception to the superficial type of root system of the other dune species was seen in *Triticum junceum*, where the longest roots penetrated some 10 cm. below the lowest recorded water level, the actual length of the roots in different specimens varying with the contours of the dune. In this connexion, attention may be drawn to Oliver's suggestion (**6**) that the distribution of *Triticum* may be influenced by the water supply, the latter possibly being one of the factors responsible for its usual replacement at greater heights on more mature dunes by *Psamma*. *Triticum* appears to be to a large extent dependent upon the ground water, and it is possible that its roots are not able to penetrate more than a certain distance, while on the other hand records show that *Psamma* may at times reach a considerable depth (**10**). Moreover, the utilization of the ground water by *Triticum*, affording a source of water of less variable salinity than the soil water of the upper layers of the substrate, may perhaps be correlated with the considerable vertical range of this species and its greater degree of salt tolerance than other associated dune species.

SUMMARY

1. The area described lies at the seaward end of the Dovey estuary, in the lee of the main dune system projecting from the south bank. A small dune is gradually developing upon the original salt-marsh vegetation from blown sand carried in through a wind-gap in the seaward dunes, and loose sand is also distributed over the rest of the area.

2. The area may be roughly divided as follows in relation to the vegetation: (*a*) the young dune itself, bearing an advance sand-dune community of which *Triticum junceum* is dominant; (*b*) the lower parts, with salt-marsh plants characteristic of the main Dovey marches, and with *Glaux maritima* dominant in the wetter parts; (*c*) the strand community, with abundant *Agrostis alba* var. *maritima*; and (*d*) the mature marram dunes to the south and west of the area.

3. A comparison of the flora of this area with that of the main Dovey marshes indicates that while the actual specific constitution of the salt-marsh communities is similar in both cases, the interrelationships and relative frequencies of the individual species are modified by the particular ecological conditions obtaining. Thus poor drainage in certain zones is thought to be responsible for the subordination of *Armeria maritima* to *Glaux* at the same tidal level as that occupied by the Armerietum of the muddy marshes, while the Festucetum and Juncetum so prominent further up the estuary are here represented only by isolated patches, being largely replaced by the encroaching dune flora.

4. The rate of accretion of new material is largely controlled by wind and tidal action, the former carrying in blown sand through the gap particularly to the young dune, and the latter depositing silt on the lower areas. In addition, the denuding action of tides and rainfall is discussed.

5. Tidal action on the area is limited to the spring tides, or other tides raised abnormally by weather conditions. It is exceptional for the entire *Triticum* dune and the strand region to be covered.

6. Ground water measurements indicated that tidal submersion has little effect upon the level of the water table more than a few yards above high water mark. The higher rainfall of the winter months maintains the ground water within a few inches of the surface in the lower parts, and continuous drainage from the surrounding dunes keeps this at a low salinity value. The greater proximity of this comparatively fresh water table to the surface in the *Glaux* zones is believed to be responsible for the difference in winter salinity conditions between this area and the *Triticum* dune.

7. An investigation of the root development of some species showed that while most of the dune species and many of the salt-marsh species possess superficial types of root systems, others are able to tap the water table throughout the year, even at its maximum recorded depth. The possession of deeply penetrating roots, allowing for the utilization of the comparatively fresh ground water, is thought to be a possible explanation of the considerable vertical range of *Triticum junceum*.

In conclusion, we should like to tender our thanks to Prof. L. Newton and to Mr E. H. Chater for the interest they have shown, and the help they have given, during the preparation of this paper.

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ON THE VEGETATION OF SEYCHELLES

By DESMOND VESEY-FITZGERALD

(*With Plates* 26–28)

INTRODUCTION

BAKER (1877), writing at a time when considerable primary forest still existed in Seychelles and while the various endemic plants were still common, has provided an invaluable account of the majority of the species. It appears, however, that he relied on collections formed by other workers and there are some curious omissions in his work. For instance, he makes no mention of *Northea* which is one of the most characteristic of the endemic trees. Since his time several new species have been discovered, chiefly by former resident collectors, namely, Messrs H. P. Thomasset and P. R. Dupont. These species were described during the early part of the present century in *Hooker's Icones Plantarum*. More recently still, other species collected by the Percy Sladen Expedition of 1905 have been described in the *Journal of Botany* and in Linnean Society publications. Finally, Summerhayes (1931) has brought the flora of Seychelles up to date in an annotated list. Since that date no new species have been described. Among all this descriptive work only the briefest references have been made to the ecology of the Seychelles flora although it has been frequently examined from the point of view of its affinities with neighbouring continents. This is a most unfortunate omission since the primary aspect of this peculiar insular flora is rapidly fading. At the present time a knowledge of its former extent and appearance rests largely on hearsay, and even the vernacular names of many of the timber trees which, two decades ago, were on the lips of every forester, are now falling into disuse. The present-day investigator longs for a week with the scientists of 1905 and even more for one day with the early explorers of the close of the eighteenth century in order to gain a glimpse of the islands as they were before the forests went down before fire and axe. On the other hand, relict patches of forest and nearly all the described species of plants are still in existence and so, handicapped as the worker must be owing to the profound changes of the past, it may yet not be too late to attempt an ecological study of the Seychelles forests. The object of this paper is an extensive survey of the existing plant communities of the colony together with a reference to their ecological relationships and an indication of their former distribution. The present contribution deals mainly with the vegetation of Mahé and Silhouette Islands. Praslin and Curieuse islands have been considered in a study of the endemic palms of Seychelles which is to be published shortly. The other inhabited islands are nowadays almost entirely under coconut cultivation, and a study of the flora of the rocky islets and outlying sand cays and coral islands will form a separate publication.

A description of the area under forest, the geology of the islands and climatic factors have been considered by other investigators and the conclusions reached have recently been summarized by Gibson (1938). It is not, therefore, intended to cover this ground again but to proceed at once to a description of the flora.

It will, however, be convenient to recapitulate briefly the known history of the islands as far as it has affected their forests. The archipelago was uninhabited up till 1744, although it appears that occasional travellers had visited it before that date. Certain species of trees, including the coconut, may have been brought by such early voyagers. Subsequent to 1744 exploitation of the native forest and the introduction of exotic plants proceeded apace. Timber was the great requirement of that age, and naturally the most accessible trees near the sea shore were the first to be cut. As the felling proceeded up the mountains, cultivation or secondary growth followed in its wake. In Mahé the introduced cinnamon dominated the secondary forest and in Silhouette *Adenanthera* seems to have been the commonest secondary tree. As these secondary forests grew up, fuel, cheap timber and charcoal could be obtained from them, and the more inaccessible blocks of native forest were only visited for specially valuable timber. Vanilla became at that time an important crop and this needed a shady environment, so forest conditions were preserved. As a consequence, denudation slowed down during the close of the nineteenth century and the older generation of to-day can remember Mahé as a well-wooded island. Early in the present century a market was opened for cinnamon leaf oil and at that time the cinnamon forests were very extensive in Mahé. Distilleries immediately sprang up in the mountains and, with little restraint, the secondary cinnamon forests were destroyed in a few years. Abundant fuel was needed for the distillery furnaces, and uncontrolled cutting took place in the hitherto untouched mountain-top forests until the very summit of Morne Seychellois, the highest mountain, was threatened with denudation. The damage done at this time was irreparable, but for a variety of reasons complete devastation was arrested at the eleventh hour. In the first place, as forest wood became scarce the distilleries were forced down to the sea-level where they used coconut trash as fuel. Secondly the Government took over and reserved large areas of ridge top. The present is an era of expensive restoration work and it is to be hoped that the last relics of the native forest will be saved for posterity.

During this final episode Silhouette fared differently. On this island *Adenanthera*, instead of cinnamon, flanked the mountain sides below the inaccessible native forest. Consequently the wholesale destruction following the "cinnamon rush" of Mahé did not take place, and fuel, cheap timber and charcoal have been obtained up to the present time from the secondary *Adenanthera* community. The native forest, on this island, is only occasionally visited for the better-class timber. Silhouette, however, is a privately owned

Phot. 1. Mountain moss forest, showing second story vegetation of *Roscheria* and *Curculigo* under a canopy of *Northea*, *Neowormia* and *Randia sericea*.

Phot. 2. Mountain moss forest, showing epiphytic growth on the buttressed trunk of *Northea* at the left and wads of moss on all the smaller branches.

estate and therefore the preservation of its interesting endemic forest is beyond State control.

Fire has not been of very great significance in the original destruction of forest in either Mahé or Silhouette, but of course, once the native forest has been cut and bracken has grown up, fire becomes a serious menace to regeneration. In Praslin on the other hand fire has been the first cause of the existing devastation.

I. PRIMARY FORMATIONS

(1) *Mountain moss forest*

The mountain forest is the only true primary plant formation left in the Seychelles. This forest is restricted in area and confined to the highest elevations. It has suffered heavy cutting of the better timber trees so that completely untouched areas are probably non-existent. On some of the more precipitous ridges and summits of Silhouette island, cutting may never have taken place. The forest covering such inaccessible places, however, is not always entirely characteristic since the soil is shallow and land-slips and storms have probably caused breaks in the canopy from time to time. Sufficient is left, however, for an idea of its primeval appearance to be gained.

The terrain upon which this forest grows is usually a steep or precipitous mountain ridge between 1800 and 2900 ft. Frequent boulders and occasional fallen trunks or large superficial roots hold the soil in place. The soil in these pockets is a rich brown colour and is composed of a sodden, slimy, spongy mass of forest debris and fibrous roots, mixed with quartz grains. It is of a very variable depth. In places it may be held by an interwoven mass of roots over a hollow cavity. Elsewhere, the layer of debris is about 8 in. deep and below this there is a bed of coarse granitic grains. Sedentary red laterite only occurs at lower elevations.

The forest is composed of evergreen trees with thick, leathery, often strap-shaped, leaves. The foliage is very dark green in colour with a reddish, almost purplish, tinge. This colour is located chiefly on the under surface of the leaves of *Northea* but the general effect is enhanced by the red on the leaves of other species, notably *Randia sericea*, by the universal red colour of the bark of all the trees and by the russet colour of the luxuriant moss-festoons. The whole effect is one of sombre gloom which is even more pronounced under the shade of the unbroken canopy of the rare patches of primitive forest which remain. Another feature of the trees growing on these steep slopes is the prevalence of stilt roots. This is probably an adaptation to dynamic conditions, either brought about by the steepness of the slopes or by the force of the drainage water rushing down the many ravines. *Northea* itself has a tendency to produce stilt roots and in the palms and *Pandani* this characteristic is most marked.

The vegetation is arranged in three stories. The canopy is formed at 40–50 ft. by the co-dominant species *Northea seychellarum*[1] and *Neowormia ferruginea*. The latter is scarcer at the higher elevations. At lower elevations the original canopy was higher, but at the present time it has been broken into by cutting and its former height is only indicated by occasional gaunt skeletons of dead trees towering above the present-day growth. The big trees tend to be spaced at about 25 ft. intervals. The second-story vegetation is composed of several species of medium-sized trees. The most characteristic member of this stage is the palm *Roscheria melanochoetes* which is common up to the highest elevations where it occasionally forms close-set stands. Two other plants which vie with *Roscheria* at the highest altitudes are the tree *Timonius sechellensis* and the shrubs *Psychotria Pervillei* and *P. sechellarum*. At a few hundred feet below the ridge tops other species are added to the second-story flora, viz. *Aphloia sechellensis* (a.); *Colea pedunculata* (a.); *Indokingia crassa* (o.–f.); *Eugenia Wrightii* (o.); *Randia lancifolia* (o.); *Erythroxylum sechellarum* (o.); the "screw pines" *Pandanus sechellarum* (o.) and *P. multispicatus* (f.–a.), and the tree ferns *Cyathea sechellarum* (a.) and *Angiopteris erecta* (f.). In the natural forest these second-story trees do not form an impassable thicket and as long as the unbroken canopy casts its shade the ground flora is not riotous. This forest-floor vegetation is composed of a variety of herbs amongst which ferns are prominent, viz.: *Nephrolepis biserrata* and *N. cordifolia*; *Lindsaya Kirkii* and *Hornei*, *Vittaria scolopendrina*, *Dryopteris Wardii*, and *Polystichum adiantiforme*. Clumps of the sedge-like *Thoracostachyum floribundum*, beds of *Curculigo sechellensis*, and such herbs as *Begonia aptera* and *Melastoma malabathricum* are also characteristic. When the canopy has been opened or destroyed the floor vegetation thickens out and dense blocks of the bracken, *Histiopteris incisa*, fill up the exposed places. Epiphytes are extremely abundant, in fact the most striking character of the formation is the sodden cushion-like wads of moss which muffle all the trunks and branches of the large trees. Besides mosses, ferns such as *Schizoloma ensifolium*, filmy ferns, the clubmoss, *Lycopodium squarrosum*, and orchids are very numerous, but this flora still awaits further investigation. There is no very clear division between the true epiphytes and the herbs which grow on the forest floor. The former descend to the base of the tree trunks and spread over the rocks while the latter may take root in the rich accumulation of humus which the epiphytic mosses hold round the tree trunks. As an instance it may be mentioned that a fair-sized specimen of the palm, *Roscheria*, has been noticed growing on a branch of *Neowormia* on the slopes of Morne Seychellois. The creeping fern, *Oleandra africana*, is common over big boulders or scrambling up sheer rock faces.

Mountain moss forest is confined to the higher ridges of Mahé and Silhouette. It is essentially the same in each island but some of the component species may be local in distribution or occur in variable frequency. More detailed collecting is needed in order to throw light on these points. As a result of the cutting down of the canopy-forming trees the herbaceous growth has become more luxuriant and the second-story trees form the new canopy of the existing forest. There is little or no regrowth of *Northea* or *Neowormia* from seedlings, due, it seems, to the smothering effect of this luxuriant growth of forest-floor herbs. It is also noticeable that any large trees of these species which have escaped cutting do not long survive after the destruction of the original canopy. The exact reason for the dying out of such trees is obscure. Certain insect pests have been suggested but it seems more likely that these highly specialized insular endemics are unable to adapt themselves to a change in the environment in which they were evolved and to which they have been attuned for so long. Below the highest ridges mountain moss forest merges into the closely allied intermediate forest which will be considered below.

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[1] If the genus *Northea* is considered to include more than one species the distribution of each has not been investigated.

Randia-Nepenthes *society*. A curious localized modification which occurs within the mountain moss forest both on Mahé and on Silhouette is the sudden incursion of the tree *Randia sericea* together with its associate *Nepenthes Pervillei*. These two species are always found together and never found separately, although the pitcher plant scrambles over other trees, such as *Northea*, so that no intimate biological connexion with *Randia* is indicated. A particularly interesting case of their invariable association is provided by the state of affairs at Delanos, Mahé. At this spot the primary forest has been destroyed by fire and the surviving forest species are now almost overgrown by "*Gleichenia* brake". The trailing pitcher plant can be seen festooned over the fern, and though the *Randia* is not at first in evidence, dwarfed shrubs are revealed when the smothering bracken is cleared away.

This society occurs at about 2000 ft. and the best examples are to be found on the high ridges of Silhouette. The *Randia* forms a sturdy tree with numerous bent and twisted branches, each branch bending so as to place its leaves to form a mosaic in a close set umbrella-like canopy the plane of which is parallel to the slope of the ground. The *Nepenthes* is very abundant, clambering over both trees and rocks and hanging down from the higher branches in curtain-like festoons. *Northea,* and to a much lesser extent *Neowormia,* persist. The former species is represented by rather small trees which are less than 40 ft. high and which have gnarled and twisted branches so that the *Northea* and the *Randia* superficially resemble each other in a curious sort of way. A reason which suggests itself for the sudden occurrence of this localized society is that the prevailing wind strikes these spots on the ridge and that the strong up-draught created by the steepness of the terrain causes a great expansion and cooling of the air with a consequent excessive development of mist, these factors creating a particular environment suitable to these species.

This society has been noticed in three restricted localities, viz. at one or two points along the main ridge of Silhouette, and in Mahé at Delanos and on the Peak Simpson-Colomes ridge.

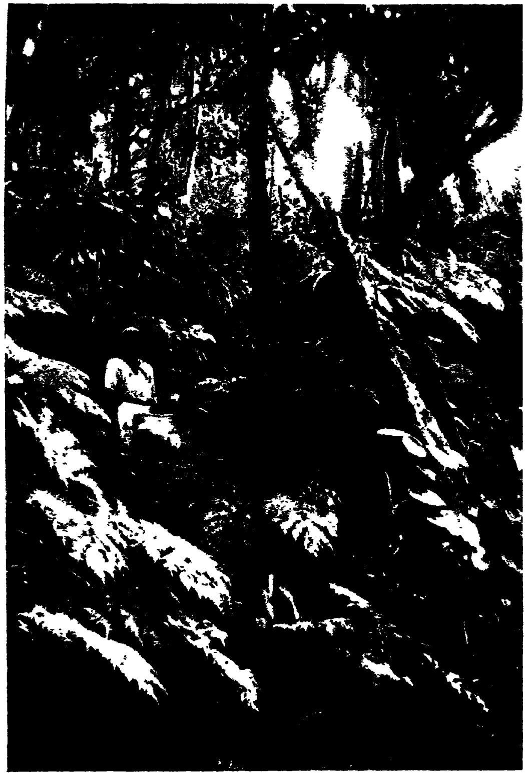
(2) *Intermediate forest*

At lower elevations than the moss forest where the soil is deeper and the site is less steep and exposed the forest is much richer in species and a very much higher canopy has developed. This forest has now been almost entirely cut down and evidence of its former appearance can only be gained from much modified scattered patches. As a result of cutting the qualitative as well as the quantitative composition has been altered and certain species which may have been of only occasional occurrence in the original communities have become abundant in the regenerating forest and vice versa. For this reason certain local variations which can be noticed in this "relict endemic forest" are appended at the end of the general description, it being uncertain if they represent a different ecological type or if they only represent different treatment in the past.

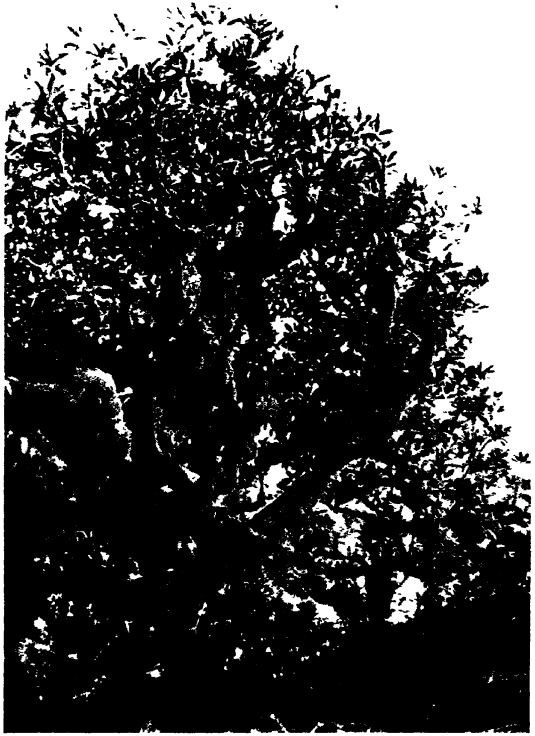
The terrain upon which this community grows is similar to that described for the moss forest, but all the characters are less extreme. The elevation is not so great and therefore mist and cloud are less frequent. The slopes are usually not quite so steep and the boulders are bigger and enclose larger pockets of soil. The soil is a sedentary laterite often of great depth. The superficial layers, however, are similar to those in the moss forest but at the present time most of these layers have been removed as a result of exposure following forest destruction, so that the underlying laterite is found more or less at the surface.

This forest was of the tropical rain forest type but unfortunately so little is left that its exact structure is difficult to judge. *Northea* and *Neowormia* were apparently the co-dominant species, these big trees being spaced at approximately 30–35 ft. intervals. Their trunks were straight and they formed a canopy at a height greater than 60 ft. Nowhere, at the present time, is the canopy intact and what other species may have reached it is uncertain, since large trees are now very rare and many of the probable species are only represented by small specimens. The reason for their destruction was the excellence of the timber obtained from these noble hard-wood trees. *Mimusops* sp. or spp., for example, are trees yielding a first class timber which is much valued locally, so that nowadays the species are only represented by rare trees, certain individuals which are, however, quite tall enough to reach the level of the canopy. *Vateria sechellarum* is also a species which is now almost extinct, but may have been a component of the original canopy at lower altitudes. Besides cutting, the general disturbance of the environment seems to have profoundly affected the larger species. It is, for example, almost impossible nowadays to find a sound example of *Northea* or *Neowormia* and in addition many of the former are parasitized by a species of *Ficus*.

In its present state of degeneration it is difficult to decide if the original



Phot. 3. Intermediate forest on the slopes of Morne Seychellois. Note the rich growth of ferns on the forest floor and the small tree of *Roscheria* above the head of the man and, in the bottom right hand corner, a sapling of *Indokingia crassa*.



Phot. 4. A tree of *Northea* on the main ridge of Silhouette Island, showing the thick cushions of moss on the trunk and branches.

forest possessed three or four stories of vegetation but available evidence strongly indicates the latter. The second tier of vegetation in this case was formed by the numerous species of trees now forming the present secondary canopy. This canopy, however, is lower than the original one since a few living and many dead giants of *Northea* tower above its level. To-day these second-tier aspects are the most conspicuous tree elements of the relict endemic forest. *Campnosperma sechellarum* (a.) and the palm *Verschaffeltia splendida* (a.) are species characteristic of this formation which do not extend into the moss forest zone. Other species present, some of which reach the higher zone but most of which become scarcer as the elevation increases, are *Colea pedunculata* (a.), *Timonius sechellensis* (a.), and *Aphloia sechellensis* (a.). The last mentioned becomes very abundant locally, especially where the ground is sloping and very rocky. In ravines the screwpine, *Pandanus Hornei*, forms localized dense clumps and on the almost sheer cliff faces *P. sechellarum* is very abundant. Both these species tend to increase after the forest has been cut. Various species of *Ficus* are also abundant especially among the huge boulders which are usually found in the large ravines. Less frequent trees which belong to this zone are *Craterispermum microdon* (f.), *Riseleya Griffithii* (f.), *Soulamea terminalioides* (o.), *Tarenna sechellensis* (f.) and *Brexia madagascariensis* (o.). Other species, some of them frequent, have not been determined.

The third tier is formed by smaller trees and saplings but there is no very sharp division between these two stories, thus no particular species can be relegated for certainty to the second or third story of vegetation. *Eugenia Wrightii*, although sometimes developing into a tree sufficiently large to reach the second tier, is more frequently found as a spindly tree, its weak stem reaching up towards the light in such a manner that the plant resembles a liane in habit. Palms are frequent, *Roscheria*, as in the higher zone, being very abundant. At lower elevations, about 1000 ft., two other endemic palms become common, viz. *Phoenicophorium sechellarum*, the larger trees of which reach the second tier, and *Nephrosperma VanHoutteana*, which at lower elevations replaces *Roscheria* as the dominant small tree of the third tier. Both palms and *Pandanus* species tend to become more abundant throughout forest from which the canopy-forming timber trees have been cut. Other trees of this tier are *Canthium bibracteatum* (a.), *Randia lancifolia* (a.), *Dracaena angustifolia*, *Euphorbia* sp. (r.), *Morinda citrifolia* (o.), which is more common nearer the coast, *Grisollea Thomassetii* (f.), *Maba sechellarum*, *Ixora pudica* (f.), *Sideroxylon ferrugineum*, *Indokingia crassa*, *Psychotria* spp., which are probably the same as those in the moss forest, *Erythroxylum sechellarum* (o.), and the tree ferns *Cyathea* and *Angiopteris*. Throughout this forest, especially in Mahé, there has been a considerable invasion of cinnamon, this species being frequent even up to the highest peaks of Mahé and at lower levels becoming very abundant until "cinnamon coppice" replaces the present formation. In Silhouette "Agati woodland" encircles and encroaches on the native forest.

The fourth tier of vegetation is composed of ground herbs. The fern, *Nephrolepis* sp., is one of the most abundant plants, but most of the species recorded in the moss forest are present, notably *Senecio sechellensis*, *Begonia aptera* and another species, *Impatiens Gordoni*, *Curculigo* sp., *Rubus* sp. (exotic), and various ferns. All these ground herbs become more luxuriant in cut forest, especially the "bracken", *Gleichenia linearis*, which in places forms dense, suffocating beds which merge into "*Gleichenia*-brake" wherever cutting has been most persistent and severe. Epiphytes are numerous but less so than in the moss forest, the moss festoons being absent. The epiphytic fern, *Asplenium nidus*, is frequent in, and characteristic of, this formation. A fern-orchid association covers exposed boulders and this rather special flora, which needs further investigation, persists in areas where the natural forest has been entirely destroyed and replaced by "cinnamon coppice" or "*Gleichenia*-brake".

Lianes are rather unusual in this forest although *Geopanax procumbens* is frequent in the forests of Silhouette where it climbs over the highest trees of *Northea* and *Neowormia* and smothers them with its foliage.

Owing to the extent to which cutting has modified the primary forest it is very difficult to discern to-day variations in its composition which may have occurred in the past. It is a fact, however, that the "relict endemic forest" has a very constant appearance over a wide extent. It is a forest composed of medium-sized and small trees, together with frequent saplings. The ground herbage and epiphytic flora is copious. The larger trees, however, show little sign of active growth and many are dying. Their regeneration is retarded by their naturally slow growth, by the scarcity of seedlings and by the choking effect of herbs and epiphytes. In their place *Pandanus sechellarum* and *P. Hornei*, and palms, *Roscheria* and *Phoenicophorium*, regenerate actively, and there is also some growth of the usual second-story species, while cinnamon becomes easily established everywhere. Much of the "relict endemic forest" is therefore a secondary *Palmetum* or else a kind of coppice of small trees and cinnamon. In ravines *Pandanus Hornei* and *Verschaffeltia splendida* form a local society, their close set stilt roots damming up the streams into pools and marshes. Certain departures from the above set type of "relict forest" are therefore worth mentioning since they may represent relics of a modified form of the primary forest, adapted to some local differences in environment.

(*a*) Excoecaria-Mimusops *society*.

The "Bois de natte", *Mimusops* sp., was an important timber tree in the past which was common throughout the islands and was probably a canopy-forming tree in the highest forest. Several species have been described, but to-day these are rare and represented only as isolated and scattered individuals at various elevations, so that the ecological affinities of each species have been lost. In certain localities, however, a species of *Mimusops* occurs as an abundant and constant associate with *Excoecaria Benthamiana* and it is difficult to avoid the conclusion that the society represents the remains of a special type of formation. A line lying N.W.–S.E. drawn across Mahé from Anse Jasmin to Pointe-à-la-Rue runs along a series of ridges including Morne Seychellois, the highest peak of the Colony. At nearly every point along this line where the elevation lies between 1700 and 2000 ft. the present society is encountered, but it has been found nowhere else. The terrain is a rocky ridge—solid slabs of considerable extent which are known locally as "glacis", and huge boulders are abundant. The soil, which is composed of quartz silt superficially enriched with forest debris, collects only in pockets, cracks and ravines. It is probable that nowhere is this deposit of any great depth. Cutting, formerly for timber and nowadays for fuel, has so altered the vegetation that a quantitative analysis is no longer possible, but the forest relics which remain are qualitatively the same as have been described above. Wherever the rock slabs are near the surface, however, both the *Mimusops* and the *Excoecaria* become abundant to the exclusion of most other trees.

(*b*) Deckenia-Memecylon *society*.

On several rocky knolls, less than 1500 ft. high, the palm, *Deckenia nobilis*, is very abundant. The best example examined is a "sugar loaf" hill above Grande Anse, Mahé, which reaches a height of 1288 ft. It is a rounded hill sloping steeply on all sides to alternating sheer cliffs and narrow ledges. On the summit are many big boulders enclosing pockets of quartz silt. This hill has no high land connexion with the central massif and the vegetation on it is very different from the *Northea-Neowormia* formation noted above. The vegetation is a relict type since cutting has been severe, the *Deckenia* itself being extensively cut for the sake of its "cabbage". The alteration has therefore been profound and a quantitative analysis is not possible. Qualitatively, however, the vegetation seems to represent a different type of formation which resembles an outlier of the dry land type of *Palmetum* encountered on Praslin.

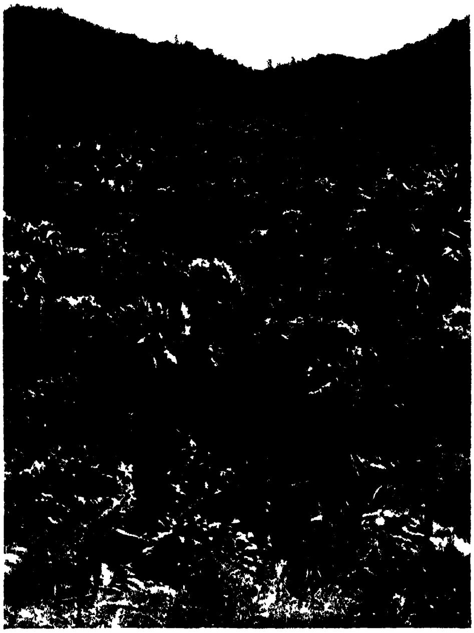
Deckenia is abundant, even though extensively cut, and it is certainly the most characteristic plant present. *Pandanus multispicatus* is also abundant in patches, but its frequency, together with the presence of blocks of *Gleichenia*, is probably a secondary characteristic resulting from extensive cutting. Other associated plants, some of which are typical of the normal rain forest but others of which are indicative of a drier type of formation, are: *Memecylon Elaeagni* (f.–a.), *Maba sechellarum* (f.–a.), *Erythroxylum sechellarum* (f.), *Timonius sechellensis* (f.), *Nephrosperma VanHoutteana* (f.), *Excoecaria Benthamiana* (f.), *Phoenicophorium sechellarum* (o.), *Randia lancifolia* (o.), *Eugenia Wrightii* (o.), *Dracaena angustifolia* (o.), *Canthium bibracteatum*, the native vanilla, *Vanilla Phalaenopsis* (o.), climbing over rocks, and *Pittosporum Wrightii* (r.). *Pandanus sechellarum*, though rare on top, is frequent on the steep sides, but the three most characteristic plants of the true rain forest, viz. *Northea*, *Neowormia* and *Roscheria*, and even the exotic cinnamon, are all rare. This knoll is at the present time isolated from the rain forest formation by coconut plantations or "*Gleichenia*-brake" so no intermediate ecotones exist. Another phase of apparently the same society is found on the steep slopes and ledges at 1200 ft. above the district known as Brillant on the east coast of Mahé. In this case, however, *Deckenia* is quite absent, due, it must be supposed, to excessive cutting in the past. The vegetation at this locality is an open dry type of woodland in which *Memecylon Elaeagni* is the dominant species. This species, mixed with a number of other elements, occurs grouped in unequal sized blocks which are divided from each other by "*Gleichenia*-brake" or bare slabs of rock. The trees average a height of 30 ft. but no shade-casting canopy is formed, and herbs, such as *Curculigo* sp., and seedlings of *Memecylon*, are abundant on the floor, which is also thickly covered with dry leaves. *Neowormia* in this case is not infrequent but this tree is cut as soon as it has grown large enough to supply a post. Immediately below these ledges, a secondary *Palmetum* of *Phoenicophorium*, *Nephrosperma* and *Verschaffeltia* becomes the dominant feature of a more normal type of relict forest.

The vegetation of Praslin is at the present time extremely difficult to study since most of the island has been devastated by fire. Much of the relict vegetation which survives consists of interesting *Palmeta* which will be discussed elsewhere. It is, however, interesting to note that some relict forest which has at least partially escaped burning is of almost exactly the same type as the *Deckenia-Memecylon* society of Mahé. The best example examined in Praslin is situated on a ridge of land lying at about 1000 ft. above the Vallé-de-Mai. Here, although the *Deckenia* is being extensively cut, this palm is abundant and still forms a close canopy at about 30 ft. in places. *Memecylon Elaeagni* (a.), *Randia lancifolia* (a.), *Erythroxylum sechellarum* (a.), the palms *Phoenicophorium sechellarum* (f.) and *Nephrosperma VanHoutteana* (f.), *Neowormia* (f.), but much cut, *Eugenia Wrightii* (f.), *Intsia bijuga* (f.), *Canthium bibracteatum* (f.), *Dracaèna angustifolia* (f.), *Sideroxylon ferrugineum* (f.), *Pandanus multispicatus* (f.) locally (a.), *Maba sechellarum* (o.), and the scrambling orchid, *Vanilla Phalaenopsis* (o.), all being the usual associates. The floor is covered with dry leaves and in more open and eroded places grow clumps of *Lophoschoenus Hornei*.

The conclusion to be drawn from all these examples is that a dry land type of forest existed on knolls and ledges, where rapid drainage through a coarse, gritty soil caused conditions of physiological dryness.

(3) *Lowland forest*

No vestige of the lowland forest has survived and the trees found along the littoral to-day are species common to the shores of most tropical islands. Up to thirty years ago some of the Seychelles Islands, such as Marianne and parts of Felicité, were still under forest at or near sea-level. These forests were visited and examined at the time by the members of scientific expeditions and



Phot. 5. Relic forest of *Lodoicea Sechellarum* in the Vallé-de-Mai, Praslin Island.

Phot. 6. View on Curieuse Island showing how erosion has followed the destruction of the original *Palmetum* by fire. The shrub at the left side is *Randia lancifolia*. The grass-like clumps are *Lophoschoenus Hornei*.

it appears from their accounts that the dominant species were "Bois de natte", *Mimusops* sp., "Takamaka", *Calophyllum inophyllum*, and "Badamier", *Terminalia Catappa*. It seems probable that in the coastal forests of the larger islands more endemic species were included, but our information on the composition and appearance of the forests must rest on the meagre accounts of ancient writers to be found in Fauvel (1909).

When the Seychelles were discovered in 1742, wood was as important a commodity as iron is to-day. The navies of the great Western European powers were ever in need of wood for shipbuilding, and navigators never lost a chance to examine in detail the timbers of new-found islands. The narratives of the early explorers are therefore full of information on the ancient forests as they saw them, and abstracts from their journals throw some light on the structure of this now extinct forest. The earliest account is that of Gossin (1742), who writes, "the seashore is lined with coconuts and is well wooded with very straight trees". and Picot (1744) adds, "there are trees in Mahé seventy feet high and fifteen feet in circumference and in Silhouette the woods are the same but smaller". Rosnevet (1786) is more detailed and he proceeds to enumerate the species which he observed, "the island (i.e. Mahé) is quite covered with forest in which are found 'bois de natte' (*Mimusops* sp.), 'bois de table' (*Heritiera littoralis*), 'badamier' (*Terminalia Catappa*), 'takamaka' (*Calophyllum inophyllum*), and 'bois de pin' (*Casuarina equisetifolia*)." Brayer du Barre (1772) adds, "the trees are spaced at 8–10 ft. from each other, they are very abundant and straight with hardly any branches or leaves for 50–70 ft. 'Lataniers' (*Phoenicophorium*) and 'palmistes' (*Deckenia*), of which the 'cabbage' is an excellent food, are abundant." Among the trees he records are "bois de natte" (*Mimusops* sp.), reaching 50–70 ft. high, "takamaka" (*Calophyllum*), 30–50 ft. high, "badamier" (*Terminalia*), "bois marée" (*Barringtonia racemosa?*), "bois de pomme" (*Eugenia* sp.), "bois jaune" (*Ochrosia borbonica*), "bois de fer" (*Vateria sechellarum?*), "gayac" (*Intsia bijuga*), and various other common coastal species such as mangroves, the latter being said to fringe the coast so thickly that only rare passages could be found through them. Morphey (1756) gives a glimpse of the structure of the forest. He emphasizes that coconuts were found only along the coast and that twenty fathoms inland there was a forest of fine trees, 15–16 ft. in circumference and more than 70–80 ft. high, dominated by two species, one a kind of "natte à grandes feuilles", evidently *Mimusops* sp., and the other with a "bark charged with a sticky gum" evidently *Calophyllum inophyllum*. Little undergrowth impeded progress through the closed forest but the steepness of the land often forced the traveller to climb with the aid of roots and lianes. The forest is said to have covered the islands to their summits but inland big trees were rarer and of a poorer quality. Frequent reference to a tree with leaves like a chestnut is believed to refer to *Vateria sechellarum*, a tree which was apparently common at lower elevations but did not reach far up the sides of the mountains. As a consequence this species is almost extinct to-day. A few specimens only survive on certain ridges of medium elevation, representing the limit of its former range in altitude. It is significant that these early accounts of the lowland forests make no mention of trees which can be identified with either *Northea* or *Neowormia*. This is a strange omission, for it seems probable that these trees grew at sea-level, because trunks of *Northea* are at the present time occasionally dug out of coastal marshes, and on Curieuse Island a species, *N. confusa*, is still found at low elevations. The various accounts agree sufficiently, however, to make it reasonably certain that the primary lowland forest was composed partly of endemic and partly of tropicopolitan species. The former predominated towards the interior and the latter towards the coast, the shore itself being fringed with mangroves. The main forest at sea-level was dominated by an endemic *Mimusops* and the widespread *Calophyllum*, two species with foliage which is superficially similar.

II. SECONDARY COMMUNITIES

(1) *Cinnamon coppice*

Cinnamomum zeylanicum Nees was introduced into Seychelles in 1769 together with many other spices. This tree spread rapidly and at the close of the nineteenth century extensive cinnamon forests are said to have existed. The early years of the twentieth century saw the commencement of the distilling industry. First bark and then leaf oil was exploited and during the ensuing thirty years the cinnamon forests were destroyed. To-day cinnamon bushes are frequent underneath coconuts down to sea-level. Cinnamon trees are frequent also in the highest mountain forests of Mahé and Silhouette. The cinnamon coppice association occurs throughout the intermediate country.

Cinnamon coppice is an unstable community from which cinnamon forest develops. The latter is, however, inhibited by continued cutting of the bushes for the distilleries. The structure of the community therefore, varies considerably according to the treatment it has received. In heavily cropped places the pyramid-shaped cinnamon bushes occur more or less widely spaced or clumped together in little groups, the interspaces being filled up with a strangling "*Gleichenia*-brake" or a suffocating "Gazontrail-mat". If the bushes are not cropped for two or three years they reach a height of 12–15 ft. and their branches spread out to shade the ground. The herbaceous flora becomes etiolated and gradually dies out. In this stage the cinnamon flowers profusely and the floor of the coppice soon becomes covered with seedlings. Closed cinnamon coppice only exists on the lands where the bushes have been reserved for several years. The finest example occurs at 2000 ft. on the Trois Frères massif. The terrain is a steep slope with an eastern aspect, boulders and rock outcrops are frequent, and a coarse-grained soil enriched by forest debris is situated in irregular pockets. Cinnamon shrubs form an irregular but closed canopy at about 20 ft., the diameter of the boles of some of these shrubs is 2 ft. Associated trees are occasional endemic forest relics and occasional exotics such as Jak. Herbs are unusual or absent under closed cinnamon coppice, and the floor is covered with dead leaves.

This community is widespread in Mahé which is the only island on which cinnamon leaf is extensively exploited. In Silhouette there are some fine cinnamon trees scattered through the forest, but there is no extensive development of the cinnamon coppice association. On the other islands cinnamon has a much more restricted distribution.

(2) "*Agati*" *woodland*

"Agati", *Adenanthera pavonina* L., is a tree which produces a useful timber and so has been extensively cut. It is, however, a species which easily regenerates from seed and therefore its very patchy distribution seems to indicate a comparatively recent introduction. This tree is rare above 1000 ft. and therefore it never occurs in any of the remaining primitive communities.

"Agati" woodland reaches its finest development in Silhouette where it seems to be becoming a climax community. A good example, subject to selective cutting but dominated by this species, covers an extensive area of medium slopes broken by frequent huge boulders between sea-level and 300 ft. at Pointe Civine. The canopy is formed at about 60 ft. by trees of *Adenanthera* (v.a.), *Terminalia Catappa* (a.), *Barringtonia racemosa* (a.), *Calophyllum* (f.), *Intsia* (f.), *Deckenia* (f.), *Ficus* sp. (o.) and "Bois de natte" (*Mimusops* sp.) (r.). There is a well-marked second-story series of various small trees and palms such as *Nephrosperma* (a.), *Phoenicophorium* (a.), *Pandanus Balfourii* (f.), *Dracaena angustifolia* (a.), *Wielandia elegans* (f.), *Morinda citrifolia* (o.), *Canthium bibracteatum* (o.), *Premna corymbosa* (o.), *Randia lancifolia* (o.) and *Ochrosia borbonica* (o.). The floor is covered with dry leaves and twigs, or irregularly broken by lichen-encrusted boulders, and there is a fairly constant but light growth of ferns such as *Nephrolepis* sp. Lianes are not usual.

This type of woodland covers the greater part of the lower mountain slopes of Silhouette up to an elevation of about 1000 ft. The community very quickly colonizes deforested areas or abandoned cultivations. The early stages of the succession in the latter case consists of a rank growth of *Panicum maximum* (a.), *Lantana* (v.a.), *Stachytarpheta indica* (a.) and *Pennisetum polystachyon* (a.). Saplings of *Adenanthera* soon become very abundant and overtop and eliminate the growth of coarse herbs. When the small trees have reached a height of about 40 ft. they form a partial canopy, but allow frequent patches of sunlight to reach the ground where a rich waist-high mat of the fern *Nephrolepis* sp. develops. A feature of a bird's-eye view of "Agati" woodland is the varying shades of green of the rounded crowns of the larger trees.

This community has a rather limited distribution in Mahé where it is chiefly represented on the heights of Anse-aux-Pins and Port Glaud and in scattered river reserves. In Praslin it is found mainly in the eastern end of the island.

(3) Gleichenia-*brake*

It is doubtful if *Gleichenia linearis* is indigenous to Seychelles but it now covers vast areas of deforested mountain land in Mahé. *Gleichenia*-brake forms essentially an early stage in forest regeneration. Under conditions of drastic forest destruction, however, it behaves as a more or less permanent subclimax. Its stability is partly due to the strangling effect its dense growth has on other vegetation and partly to the continued cutting of regenerating cinnamon for distillation and other woody growth for fuel.

Some of the wider stretches of "brake" occur on hill tops above 1000 ft. in the La Misere district of Mahé. The terrain in this district is composed of slopes of eroded red soil or hill tops composed of huge boulders enclosing pockets of quartz silt. The *Gleichenia* forms an impenetrable growth, the erect green fronds reach a uniform height of 6–8 ft. and arise from a compact mattress of dead and dry fronds, stipes and rhizomes. Tree growth may be completely absent over wide stretches or it may be represented by scattered or frequent coppiced shrubs. In the worst places all timber trees are non-existent except for occasional small specimens of *Neowormia*. The species usually represented are members of the second-story zone of the endemic forest together with cinnamon. In the better kept land relict forest trees tower above the bracken, but there is, even here, little chance for seedlings to make much headway.

This community occurs, but is less general, in Silhouette, where the endemic forest is either still standing or regeneration has proceeded to the Agati-woodland "climax". In Praslin "*Gleichenia*-brake" is hardly represented at all.

(4) Panicum-*mat*

The grass, locally known as "Gazon trail", *Panicum parvifolium*, is apparently a plant which has been introduced into Seychelles during recent years. It appears to be spreading fan-wise over the worn-out land behind Victoria, the centre of the densest population. This grass occupies a zone below the "*Gleichenia*-brake", that is, below 1000 ft. down to sea-level. It covers land where, owing to a comparative scarcity of rocks, erosion of the humic soil and general impoverishment of the land have taken place. A form of shifting cultivation is practised over the hillsides of Mahé, and after the crops, usually cassava and sweet potatoes, have been harvested, weeds are allowed to take possession of the land. If the soil is not too worn out a rank growth of *Panicum maximum* and *Lantana Camara* becomes established. This, as has been explained above, forms an early stage of forest regeneration. Subsequent cultivation, however, will impoverish the soil, and the resulting weed growth under these circumstances is characterized by such species as *Stachytarpheta indica, Paspalum paniculatum, Pennisetum polystachyon, Turnera ulmifolia, Dianella* *ensifolia*, *Elephantopus scaber*, the fern *Nephrolepis biserrata*, and the club-moss *Lycopodium cernuum*. This community holds the land for some time but forest regeneration is very slow since the soil is too impoverished to support both herb and tree growth. In the presence of *Panicum parvifolium* the above-mentioned mixed herb mat is rapidly replaced. At first the trailing stems of the grass encroach into the more open places. Next the various species of the herb mat become reduced in vigour and size, and when they no longer cover the ground the *Panicum* makes rapid inroads and soon the last of the mixed herbs vanish from the block colonized by the *Panicum*.

The only plant which is able to tolerate the smothering close-set mat is the little ground orchid, *Cynorchis fastigiata*, which pokes its flowers up through the grass. Any bushes or shrubs which may exist are choked by the grass and they make no growth. If they receive a set back such as being cut to provide fuel they die out altogether. Once established the *Panicum* mat behaves as a stable community and it is most difficult to eradicate. Hoeing up is of little use since the grass re-establishes itself much quicker than any other plant. The only way to replace the grass is for constant nursing and attention to be given to young trees until they are able to shade the ground, when the *Panicum* will automatically die out. In view of the difficulty with which this grass is eradicated its spread is a very real danger, and great care should be taken when "*Gleichenia*-brake" is cleared that reafforestation work is put in hand immediately, otherwise *Panicum*-mat may take possession of the land and future work will be much more difficult. The only useful purpose which can be accredited to this community is that it very effectively prevents soil wash from large areas of abandoned land. Where the soil has suffered very severe erosion down to the hard red subsoil, *Panicum*-mat does not become established. For this reason the community is not represented over the burnt hillsides of Praslin. It is quite possible that if this grass had been present in Praslin at the time the island was first devastated, the damage due to soil erosion would have been very much less. *Panicum*-mat must, therefore, not be classed as a pest but rather as a sign of gross mismanagement of the land.

III. PRACTICAL CONSIDERATIONS ARISING FROM A STUDY OF THE VEGETATION

It is not the purpose of this paper to enter into details of forest regeneration and land management. Active measures for reafforestation have been undertaken by the Department of Agriculture during recent years (see Annual Reports, 1934–8), and the whole subject has been dealt with by Gibson (1938). Certain fundamental principles, which may not be fully appreciated, are, however, emphasized by a study of the existing plant formations and it is necessary that these be kept in mind if a successful programme of reclamation is to be pursued.

Forest degeneration over the areas under consideration is manifest in three rather distinct stages, and each of these stages calls for different treatment if successful and economic regeneration is aimed at. The characteristics and the methods of restoration of each stage are best considered separately. The various plant communities represented have already been dealt with and so they may be simply referred to by name. Before, however, forest regeneration can be considered, soil reconstruction must be attended to. In the natural forest the "soil" is separated into distinct layers. (1) A superficial layer of recently fallen, dry but little changed leaves and other plant debris. (2) A rather thick, spongy layer of rotting vegetable matter in which fungal decomposition is active and which has a rather acid reaction. (3) The actual mineral soil which is either a bed of quartz silt or else sedentary laterite. The latter is itself subdivided into the following horizons: (*a*) a superficial horizon stained a dark colour with humus, (*b*) an intermediate lighter coloured horizon with a rather friable texture and (*c*) the disintegrating parent granitic rock set in a matrix of a very sticky red "clay". Very frequent boulders and solid superficial unchanged rock are characteristic features in Seychelles which profoundly modify the above zonation. Forest degeneration is usually accompanied by soil degeneration, and the destruction of the layers of vegetation results in the loss of one or more layers of the soil. In extreme cases all vegetation is absent and the layer of disintegrating parent rock is exposed at the surface.

The least extreme stage of forest degeneration is that which has already been referred to as "Relict endemic forest". In this the original native forest has been "combed" through for timber and all suitable trees have been cut out. The canopy has thus been destroyed and in fact the only "top-story" trees which were left were probably the unsound ones. To-day these only remain as scattered dying giants or gaunt skeletons towering above the present-day forest-roof. The "second-story" trees are left to form a light canopy and the natural floor flora soon becomes rampant. The soil under these conditions remains essentially intact.

Regeneration to the original forest appears never to have taken place. This may be due to the fact that the dominant hardwood species, being very slow-growing, have not had time to re-establish themselves. It is more probable, however, that the original formation, being one of very long standing and having been evolved under very peculiar and isolated conditions, is quite unable to maintain and reinstate itself under the modified environment when once the original stability of the forest has been interrupted. In the case of *Northea* healthy seedlings and young trees are most unusual, though it is quite possible to grow good trees if they are cared for in the same way as an exotic timber tree. *Neowormia* seeds freely and seedlings grow vigorously but appear quite unable to stand against the severe competition with the congested "floor" growth natural to cut forest. Regeneration is limited to a slow growth and thickening of the small and medium-sized species originally forming the "second-story" zone of the forest. *Northea* and *Neowormia* are prominent in the light canopy formed, but they are almost entirely represented by unsound trees which can never overtop the second growth. The most rapid growers are the palms and certain species of *Pandanus* and these therefore become very prominent, a secondary *Palmetum* often being the result at all medium elevations.

In the light of the above conclusions it cannot be too strongly emphasized that any areas in which the original canopy remains intact should be rigorously reserved from all future cutting. This point is of the utmost importance in view both of the unique nature of the forests of Seychelles, and owing to the fact that these forest remainders clothe ridges on which it would be extremely difficult to establish any other type of forest. In such areas where the canopy has gone but the soil still remains intact, valuable reafforestation work is possible. This work will be most successfully accomplished by following and aiding the natural succession. By following the succession, the introduction of desirable species (planting the more valuable kinds and broadcasting the less valuable ones) natural to the association is implied. Aiding the succession implies judicious slashing of the floor growth which will otherwise be only slowly suppressed by the tree growth; and restricted cutting of the faster growing but useless palms and *Pandani* which will otherwise successfully compete with the more valuable timber trees. Some of the very valuable hard woods should repay individual attention during their earlier years, but perhaps the quickest and most paying policy to adopt is the broadcast establishment of *Adenanthera* up to at least 1500 ft. elevation.

More drastic and continuous cutting has resulted in the complete elimination of the original communities, the members of which only linger on as scattered trees and, in the face of competition, the original forest is quite unable to re-establish itself. As a further consequence the "soil" is modified by the complete or at least partial destruction of all layers above the mineral soil. Under these circumstances an entirely different community becomes established, namely, any one of the "secondary communities" already noticed. In the more favourable instances this may be "Cinnamon" or "Agati woodland", or local blocks of exotic *Albizzia*, *Pterocarpus* and *Eugenia*. If this secondary development is interfered with the vegetation is represented by an earlier stage such as "*Gleichenia*-brake". As has been indicated earlier, the latter, once established, may be permanent under present conditions.

Reafforestation under these circumstances may be accomplished by stimulating the progress of the natural succession, i.e. eliminating the "brake" and allowing the woodland to come in. If set about in the right way the "brake" is easy to destroy, the essentials to be considered being the following: the bracken must be cut *below* the creeping rhizome so that new shoots from the old plant are prevented from growing. The soil must be exposed for the reception of the seeds of the subsequent vegetation. This is best achieved by rolling the cut mattress of fern into contour "bunds", a method which has the added advantage of preventing erosion before the new growth becomes established. Lastly the seed of the required woodland must be available, and if no mature trees of the desired species are at hand seeds of these should be sown. By working with the succession in this way reafforestation is easy, cheap and fairly rapid.

The value of the reinstated forest may be increased by planting timber trees not natural to the community. If this is attempted it must be realized that the very advantages of ease, economy and speed attendant to the establishment of the natural climax, mitigate against the successful establishment of these more desirable but less adaptable species. The forester is working now *against* the succession. Competition will be severe, and if success is to be achieved he must be prepared to bear the cost of continual attention to the young trees until they are very firmly established.

The worst stage of deforestation has taken place under rather particular conditions. As has been already noticed, a dry type of forest largely dominated by palms occurred on the hillsides of Praslin and Curieuse. These forests were combed through for timber, but regeneration of the *Palmetum* was vigorous. The forest was, however, extremely inflammable (the same remarks apply to the other types of forest when reduced by cutting to the "*Gleichenia*-brake" stage), and fire razed it to the ground. In the temporary absence of vegetation, especially under conditions of continual burning, where there are few boulders, soil wash is excessive and erosion continues until even the horizon of raw rock is exposed and scored into gullies. The hard, baked, exposed soil is unsuitable even for the establishment of "brake", *Gleichenia*, in common with all ferns, needing an ample amount of moisture for the development of its initial prothallus.

Under these conditions any reafforestation programme must, of necessity, be preceded by the reconstruction of the soil structure and fertility. The most pressing necessity is the arresting of gullying and wash. This can only be accomplished by the establishment of dams and contour pits in which silt can be collected. Subsequently some form of vegetation must be established which, by aiding the retention of moisture, providing shade, loosening the soil and supplying humus, will further aid soil reconstruction. In this connexion it must be noticed that any form of vegetation, even "brake", is desirable in the early stages. Further treatment comprises working in unison with and encouraging the course of the natural succession. The most important considerations in this connexion is to prevent any set back such as a fresh fire. Fire breaks and fire restrictions are of the utmost importance. The next consideration is the supply of seeds of desirable or suitable species. In this way theoretically forest could be built up along lines indicated above. In practice, however, the soil may have become so poor that the effect of the competition between the initial ground-cover plants and the subsequent tree growth may entirely arrest the course of succession. In any case when land has once been allowed, through ignorance and neglect, to degenerate to such a deplorable state, the forester must be prepared to face an expensive and long-drawn-out campaign before any results are obtained.

To recapitulate briefly. A study of the vegetation of Seychelles emphasizes the following important practical points of forest management under local conditions.

(1) If the native forests are to be preserved the few remaining areas must be immediately reserved from all forms of exploitation.

(2) The reafforestation of the large areas of uneconomic mountain land can be accomplished cheaply by urging forward the progress of the natural succession. "*Gleichenia*-brake" must be replaced by woodland. *Adenanthera* and cinnamon and to a lesser extent *Albizzia* sp., *Pterocarpus* sp. and *Eugenia* sp. are all common exotic species which form climax woodlands. Plantations of more useful timber trees, while very desirable, should only be set out if the forester is prepared to see the programme through. To neglect a plantation of this nature before the young trees are established sufficiently to form a woodland formation of their own is tantamount to wasting the time and money spent on its initial establishment.

(3) If worn-out and eroded hillsides are to be saved, time and money at least commensurable with the waste and neglect of the past is necessary before success can be achieved. In these cases the soil fertility and even the soil structure must be reconstructed before the natural plant succession can become established.

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EXPERIMENTS WITH POND MUDS

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(*With one Figure in the Text*)

The algal ecology of ponds is a complex problem in which many factors are involved. Attempts have been made to correlate the periodicity of the algae with climatic conditions and with changes in the chemical composition of the water, but each of these offers only a partial solution of the problem.

An important factor which has received little attention must be the nature of the mud which lines the bottom of the pond and the interchanges which take place between the mud and water at the mud surface. The decaying remains of plant and animal tissue form decomposition products which diffuse into the water, while at the same time the activities of micro-organisms gradually deplete the oxygen supply.

It is further likely that there is considerable base exchange in most muds, such ions as iron and calcium being replaced by those of ammonia, and there will also be variation in the extent to which certain substances are adsorbed and held by the colloids in the mud.

It is clear, then, that at the surface of the mud there exists a constantly changing system, and analysis of the water from the surface of the pond may give little indication of what is going on at the bottom. Yet it is in the mud that the resting period in the life of most algae is spent, and it is largely on the extent to which germination of zygotes and oospores occurs that the growth of algae in the pond depends. It is a well-known fact that they may germinate readily to give a good growth of algae the following season or they may lie dormant for several years. The production of maxima is undoubtedly connected, in part at least, with the existence of suitable conditions at the mud surface for the germination of the resting spores of the algae concerned.

OUTLINE OF EXPERIMENTS

Mud from three types of pond was studied. *Longshaw* is situated at about 1000 ft. in a moorland area, with *Nardus* and *Eriophorum* on one side and a mixed plantation on the other. The bottom is very peaty and supports a considerable growth of *Potamogeton natans* and *Callitriche*. The water has a *p*H of 6·4–6·8.

Ford is situated on the Coal Measures and surrounded by agricultural land. The bottom is of black organic mud supporting *Elodea*, *Potamogeton* and *Callitriche*; *p*H of water 7·2–8.

Shireoaks is situated on magnesium limestone, has a calcareous mud supporting *Chara, Hippuris* and *Ceratophyllum*; *p*H of water 8–8·6.

As far as possible surface mud was collected, though some of the deeper mud was inevitably included. Samples were set up in large glass jars, each jar containing 1½ in. of mud and 1½ l. of water which were thoroughly shaken together and then allowed to settle. Two series were tested, one from which all leaf mould and twigs had been removed, and a second to which a layer of leaf mould was added after the mud had settled. Siphons were fitted so that the water for analysis could be drawn off from the mud surface without undue disturbance, and the jars were kept in the north window of a cool room. In each series an extra jar was included with a thin film of paraffin on the surface to produce relatively anaerobic conditions for purposes of comparison. At intervals of a fortnight water was drawn off from one jar of each series for analysis. The experiment lasted 6 weeks and the results of analysis are shown in the table and graphs.

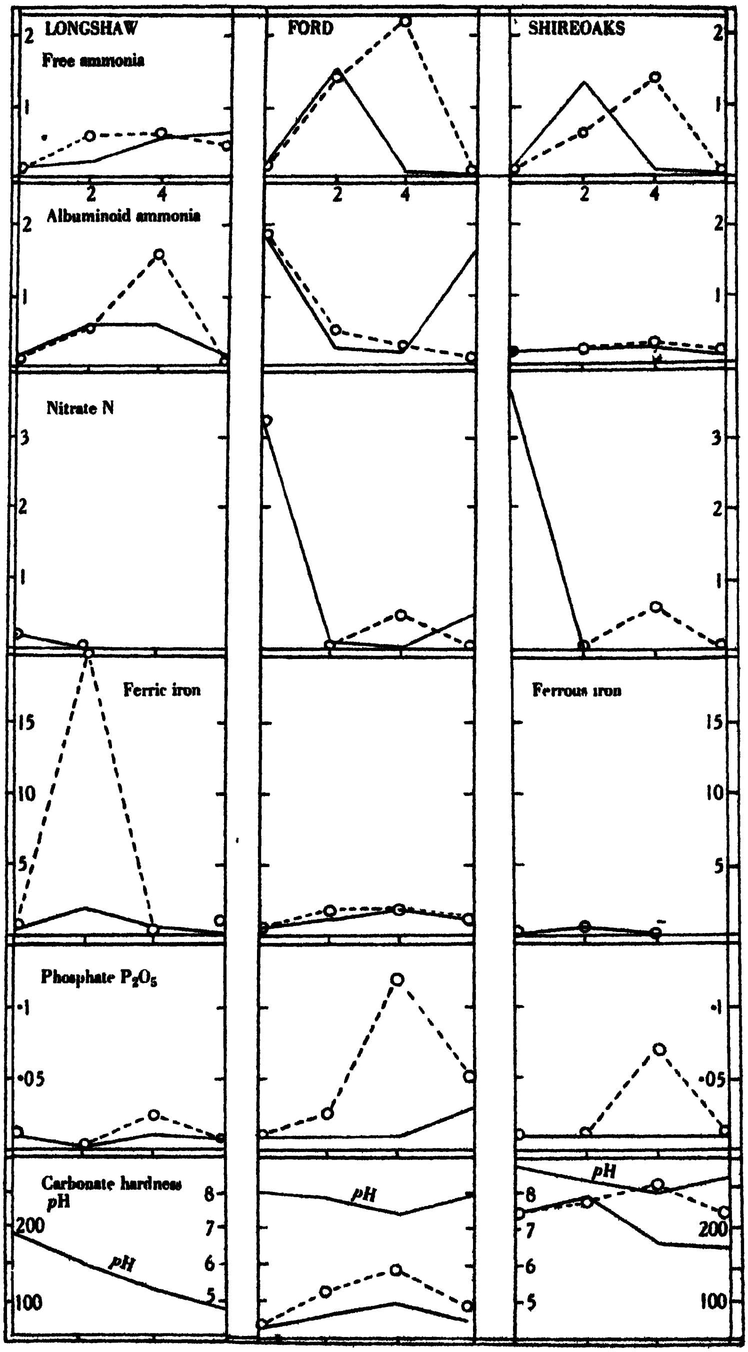
Composition of the water from the three series of jars at intervals of 2 weeks. Quantities in mg. per litre

	Original water	After 2 weeks		After 4 weeks		After 6 weeks		Anaerobic 8 weeks	
			L.M.		L.M.		L.M.		L.M.
				Longshaw					
Temp.		11·2	11·2	11·3		11·8			
*p*H	6·8	6·0	6·0	5·35		4·7		4·78	
Nitrate N	0·1	Trace	Trace	—	—	—	—	Trace	—
NH_3 free	0·095	0·2	0·55	0·55	0·59	0·58	0·45	Trace	—
Albuminoid NH_3	0·138	0·5	0·5	0·6	1·65	0·162	Trace	0·169	0·175
Phosphate P_2O_5	0·01	Trace	Trace	0·01	0·025	0·006	0·0065	0·01	0·006
Ferric iron	0·36	1·87	20·4	0·565	Trace	—	1·07	-	—
Carbonate	—	—	—	—	—	—	—	—	—
				Ford					
Temp.		8·0	8·0	11·2	11·2	11·3	11·3	12·8	12·8
*p*H	8·2	7·8	7·8	7·4	7·6	7·8	7·9	8·0	7·9
Nitrate N	3·3	0·125	0·08	Trace	0·5	0·5	Trace	—	—
NH_3 free	0·112	1·5	1·4	0·065	2·21	—	—	Trace	Trace
Albuminoid NH_3	2·5	0·265	0·5	0·212	0·358	1·57	0·15	0·2	0·4
Phosphate P_2O_5	0·01	0·013	0·028	0·015	0·125	0·036	0·05	0·007	0·077
Ferric iron	0·32	1·13	1·78	1·7	1·79	0·98	1·25	-	4·3
Carbonate	62·0	80·0	112·0	86·0	148·0	67·0	96·2	114·0	158·0
				Shireoaks					
Temp.		8·0	8·0	11·2	11·2	11·3	11·3	12·8	12·8
*p*H	8·6	8·3	8·3	8·0	7·9	8·4	8·2	8·2	
Nitrate N	3·6	—	0·075	—	0·63	—	Trace	—	—
NH_3 free	0·075	1·25	0·65	0·1	1·4	—	0·075	—	—
Albuminoid NH_3	0·22	0·25	0·25	0·25	0·275	0·162	0·175	0·3	0·2
Phosphate P_2O_5	0·01	0·01	0·01	0·01	0·062	0·01	0·01	0·03	0·015
Ferric iron	—	—	-	—	—	—	—	—	—
Carbonate	208·0	254·0	246·0	180·0	262·0	172·0	228·0	254·0	264·0

METHODS

The estimation of ammonia, nitrate and phosphate was carried out by methods described in a previous paper (Lind, 1938).

Iron was determined by the method of Marriott & Wolf (1906) as employed by Hopkins & Wann (1926). To 2 c.c. of the conc. HCl were added 20 c.c. of



Variation in dissolved substances and pH in the water from jars of the three series during 6 weeks. Quantities in mg. per litre. Plain line: without leaf mould. Dotted line: with leaf mould.

10% KCNS and 28 c.c. of the water to be tested, and the whole was made up to 100 c.c. with acetone. The standard used was a solution of $FeNH_4(SO_4)_2$ in water, and comparison was made in tall graduated glass cylinders.

Carbonate hardness was estimated by titrating 25 c.c. of the water against $N/100$ H_2SO_4 using as an indicator a mixture of 0·04% bromo-cresol-green and 0·026% methyl red in 60% alcohol.

Hydrogen-ion concentration was determined electrometrically.

NOTES ON RESULTS

Nitrate. At the time of collecting, nitrate was high in Ford and Shireoaks and low in Longshaw. In each case at the end of 2 weeks it had fallen to the neighbourhood of 0·1 mg. per litre. This level was maintained at Ford, rising again in the fifth week. In the other two waters, however, the quantity remained too small to estimate accurately by the phenol sulphonic method when the water was at all brown. "Trace" means below 0·05 mg. per litre. This sudden decline in nitrate is also seen under natural conditions in ponds during the summer, but in the latter case it is replenished by supplies introduced by drainage water (Lind, 1938).

Ammonia. The fall in nitrate in the first 2 weeks was each time accompanied by a rise in ammonia which was maintained at Longshaw, but in the other two showed a sharp decline with none detectable at the end of 6 weeks.

Briefly, then, after the initial rise in ammonia there was a sharp decrease in inorganic nitrogen as the experiment progressed. This was not due to the growth of algae which were inconspicuous at the time. The rise in ammonia due to the decomposition of organic material was more pronounced and lasted longer in the jars containing leaf mould. Its decline might be attributed either to its conversion into nitrate or to its adsorption by the mud. The latter is evidently the case except at Ford and in the presence of leaf mould where both factors probably operate.

The sharp decline in nitrate is more difficult to explain. Under anaerobic conditions denitrifying bacteria might be responsible, but the potential at a platinum electrode at the mud surface showed that oxidizing conditions were maintained throughout the experiment (Pearsall & Mortimer, 1939). If, however, the nitrate were adsorbed swiftly into the deeper anaerobic layers of the mud it might be reduced to gaseous nitrogen and lost.

Phosphate. The amount of phosphate was approximately equal in all three sets of jars and remained fairly constant. The presence of leaf mould increased the phosphate content considerably in each case.

Iron. In Longshaw and Ford the ferric iron increased slightly at the beginning of the experiment and then fell off and was absent after 6 weeks. A strong deposit of ferric hydroxide developed on the mud surface in the Ford jars and to a much slighter extent in Longshaw, but in Shireoaks jars ferric iron was absent both from the water and the mud surface. The presence of leaf mould made a great difference and the iron in Longshaw then increased 50 times in a fortnight.

After 3 months, mud from each of the jars was tested for replaceable iron by Misra's modification of Comber's test (Misra, 1938). In no case was ferric iron detected, although it was evidently there as a precipitate in two of the muds. The addition of two drops of HCl liberated ferric iron in Longshaw and to a greater extent in Ford. In both muds there was also considerable iron in the ferrous condition, and this was true even of Shireoaks but only in the bottom mud.

Base exchange. It is clear that from the point of view of base saturation the ponds fall into a series beginning with Longshaw and culminating in Shireoaks. Part of the ammonia formed as a result of decomposition of organic matter is adsorbed on to the mud particles replacing the cations already present. In the unsaturated Longshaw mud this results in liberation of iron and of hydrogen ions as shown by the increased acidity of the water as the experiment progressed. The fact that no iron was detected in the water at the end of 6 weeks, although ammonia was still present, suggests that all the iron had already been replaced and then precipitated as an insoluble ferric salt. This is also in accord with the gradual increase in ammonia in Longshaw in contrast to the sharp decline in the other two. The ammonia maximum in Ford corresponds with the highest figures for carbonate hardness, ferric iron and acidity. In Shireoaks, while a little ferrous iron appeared, it was mainly the ions of calcium and magnesium which were replaced giving a considerable increase in carbonate hardness. In a previous experiment, carried out in February, ferric iron was found in the Shireoaks water and the mud surface became brown, especially in the anaerobic jar. This is difficult to understand unless it is in some way connected with the activities of the sulphur bacteria which were very plentiful at the time.

Effect of leaf mould. The effect of leaf mould was most clearly seen in the continued production of ammonia for 4 weeks instead of 2, the maximum being accompanied by a rise in nitrate following on the initial depletion. Neither of these maxima was seen in Longshaw, possibly owing to the rapid absorption of ammonia by the unsaturated mud resulting in the liberation of unusual quantities of iron, or to a deficiency of nitrifying bacteria in the more acid water. There was also a marked increase in phosphate when leaf mould was present. It is clear that the annual leaf fall must be a factor which materially affects the chemical composition of pond waters.

Productivity. A second set of jars, set up in the same way as the experimental jars, was kept in a sunny window in the laboratory and the productivity of the muds noted.

Longshaw mud was on the whole unproductive. A scum of diatoms, mostly *Surirella*, appeared round the walls of the jar, and a slight growth of *Micro-*

spora, *Mougeotia* and *Oedogonium* developed, together with a few desmids. It should be noted that in this series ammonia was present throughout the experiment but nitrate was absent after 2 weeks.

Ford was more productive although the strong deposit of ferric hydroxide on the mud and on the sides of the jar and the metallic film on the surface did not look conducive to growth. At first a scum of *Oscillatoria* developed all over the surface and sides of the mud and a few sulphur bacteria were found. Only after 7 weeks did any considerable growth of Chlorophyceae appear, chiefly *Spirogyra* and *Rhizoclonium*, and then only in the jar containing leaf mould. This was at a time when the nitrogen content of the water was very low.

Shireoaks. The most striking feature of this mud was the strong growth of sulphur bacteria which appeared early in the experiment. *Beggiatoa* formed a cobwebby scum on the mud surface, and *Achromatium* was common deeper in the mud. Both were especially prevalent in the leaf-mould jars. In addition, there was at first a very little *Oedogonium*, *Tribonema* and *Mougeotia*, but again, after 6 weeks, *Rhizoclonium*, *Cladophora*, *Oedogonium* and *Spirogyra* became common and plants of *Chara* appeared. This water was probably most productive.

Anaerobic jars. It was noticeable that the growth of algae was often greater in the anaerobic than in the aerobic jars. In Ford, in the cool culture room beneath a film of oil, grew a dense scum of Cyanophyceae together with *Ophiocytium*, *Chlamydomonas*, *Euglena* and various other unicellular forms. On the mud surface where there was no iron deposit, *Navicula* spp., *Microcystis* and *Microthamnium* were found. The difference was most marked in the leaf-mould jars where a considerable growth of *Oedogonium*, *Spirogyra* spp., *Mougeotia* and diatoms appeared as well as a scum of blue-green algae. The same greater productivity of the anaerobic jars was noticeable in the Shireoaks series. Actually, the cultures were not completely anaerobic, for a Winkler test at the end of the experiment showed the water to be still half-saturated with oxygen. The inorganic nitrogen, however, was very low.

This comparison of jars kept under laboratory conditions does not reflect truly the natural productivity of the muds. From a study of the ponds themselves, it is clear that Longshaw is more sterile than the other two and that Ford is the most productive.

SUMMARY

A series of reactions go on at the mud surface in ponds, which may be of importance in providing the conditions necessary to the germination of algal spores.

The reactions fall into two categories: (*a*) decomposition of organic material by micro-organisms resulting in the liberation of ammonia and nitrates; (*b*) adsorption of ammonia by the mud particles with liberation of exchangeable bases. While the balance between these two sets of reactions at

the mud surface, together with the amount of available oxygen, and temperature, may be important in determining germination, the amounts of inorganic nitrogen and soluble bases in the water resulting from them will affect the growth of algae subsequent to germination.

The inorganic nitrogen in the water is seriously depleted in the first month of the experiment in saturated muds, the initial nitrate having all disappeared after 2 weeks. The loss of ammonia can be partly explained by adsorption, and the decrease in nitrate would appear to be due to denitrification possibly going on under anaerobic conditions below the mud surface.

The carbonate hardness, iron content and hydrogen-ion concentration of the water vary with the extent to which ammonia is available to replace the respective cations.

The presence of leaf mould brings about a continued production of ammonia and often a second low nitrate maximum, increased phosphate, and in unsaturated muds, much increased replaceable ferric iron.

The productivity is in all cases greatest after 6 weeks, the unsaturated muds being least productive. The growth of algae continues when neither nitrate nor ammonia can be detected in the water.

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E. M. LIND

REVIEWS

THE JOURNAL OF ANIMAL ECOLOGY

Vol. 9, No. 1, May 1940.

This number contains nine original papers, eight reviews, 149 Notices of Publications on the animal ecology of the British Isles, and the report of the Society's meetings and business. In order to provide against increase in the cost of production due to the war, certain economies have been effected: in particular the address list of members has been omitted, and free duplicate copies of the Notices are no longer issued with the *Journal*, although they are still obtainable by separate subscription. Otherwise, apart from a slight reduction in size and in the number of plates, the *Journal* is much the same as usual.

There is a study of the population dynamics of young salmon in the River Eden, by K. Radway Allen. C. Teesdale shows that very low density in a tsetse fly population in East Africa does not prevent the males and females from finding one another, and therefore that the population is unlikely to die out from this cause when reduced to such low levels. P. H. Leslie and R. M. Ranson record the life curve and reproductive rates of a laboratory population of voles, *Microtus agrestis*. By allowing for the natural mortality under probably optimum conditions they are able to give the maximum natural rate of increase of a vole population: most previous calculations of increase of rodents having ignored the basic mortality shown in the life curve. It is also proved that the vole lives on the average for not more than about 34 weeks.

M. K. Colquhoun describes the results of bird counts in a mixed deciduous wood in Berkshire, and the relation between walking counts and absolute census, bringing out the importance of the relative conspicuousness of different species and of the walking speed of the observer. He also gives some other counts for Savernake Forest. J. M. Winterbottom gives a somewhat similar discussion based upon his experience of walking counts of birds in Northern Rhodesia. H. P. Moon analyses the results of observations in Lake Windermere upon the movements of freshwater invertebrates, which showed continual local movements that were greater at night. Averil Morley's paper on recolonization of burnt woodland (various types) by birds is a useful addition to our small stock of information about ecological succession of animal communities in Britain.

Vernon D. Van Someren made an elaborate investigation of the factors affecting the degree of rising of trout in a small piece of water in Surrey, from which he shows that low temperature is very important in stimulating rising, as also are some other factors such as the hatch of "fly". Light is also important in determining the hours of rising.

J. Richard Carpenter presents a comprehensive historical survey of insect outbreaks in Europe, based upon published records of various kinds. This monograph includes a summary of the state of organization of recording in different countries, the main trends of reported outbreaks, and some discussion of the manner in which outbreaks happen, together with a valuable bibliography.

Reviews cover three American books on (chiefly animal) ecology, economic insects, the littoral fauna of Great Britain, animal keeping, and the life of American animals in winter.

Charles Elton

THE FENS

Darby, H. C. (i) *The Medieval Fenland.* Pp. xvii+200, with 11 plates and 25 maps and diagrams. Price 12*s.* 6*d.* (ii) *The Draining of the Fens.* Pp. xix+312, with 31 plates and 34 maps and diagrams. Price 21*s.* (Cambridge: The University Press.)

Though little of it is now left unchanged, the Fenland at one time must have been one of the most striking geographical and biological units in the British Isles, just as it still remains one of the most remarkable agricultural and economic features. Its interest in these respects is very great and from these points of view its history is of the utmost value in helping us to picture it in its former extent and original character. From another aspect also the Fenland is remarkable. Lying near to the main lines of human and of animal invasion and showing considerable diversity of terrain and soil type, it is a region of great interest in showing the way in which these factors have affected the development of human life in the area, while the existence of extensive and recent sedimentary deposits is of the greatest assistance in reconstructing the chronology. It is from this second point of view—almost that of human ecology—that Dr Darby has treated the history of the Fens, and he is to be congratulated upon two volumes which possess almost as much general interest as their value in relation to the story of the economic development of the region.

The first of the two volumes deals with the Fenland as it was roughly from Romano-British times until about the end of the fifteenth century. Naturally much is made of the conditions at the time of the Domesday Book and the developments are traced mainly by contrasting statistics derived for this period with corresponding data for some two hundred and fifty years later. After the latter period the Fens entered on a phase when their history was concerned mainly with their draining. To this phase the second of the two volumes mentioned is devoted. It is concerned mainly with the various projects and methods of draining and with their effects upon the economic activities of the inhabitants. It concludes with a summary of the difficulties, engineering and administrative, which have been bequeathed to the present generation by the activities of the last two or three hundred years. While neither of these volumes is primarily ecological, each contain much that is necessary to any general ecological picture of the Fen country and data that will prove invaluable to many other lines of study.

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